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THE AMMONITE SUBFAMILY
LABECERATINAE SPATH, 1925:
SYSTEMATICS, PHYLOGENY, DIMORPHISM
AND DISTRIBUTION
(WITH A DESCRIPTION OF A NEW SPECIES)

By
HERBERT CHRISTIAN KLINGER

Cape Town

Kaapstad

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SYSTEMATICS, PHYLOGENY, DIMORPHISM AND DISTRIBUTION
(WITH A DESCRIPTION OF A NEW SPECIES)

By

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Cape Town*

(With 18 figures)

[MS accepted 20 October 1988]

ABSTRACT

Systematics of the subfamily Labeceratinae Spath, 1925, are discussed. Data from Zululand suggest that the subfamily probably consists of a single, dimorphic genus, to which the names *Labeceras* and *Myloceras* have been applied. Distribution of the subfamily shows concentration in two main areas—southern Africa—Madagascar and Australia. Comparisons of the faunas of these suggest a high degree of endemism, and also show that post-mortal drift is negligible. Absence of labeceratine faunas from the south Atlantic—with the exception of a single locality in the Austral Basin of southern Patagonia—may possibly be linked to the opening of the Atlantic and the associated different environments, but also the differential ecological requirements of the different ammonite taxa, of which we know nothing.

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INTRODUCTION

The ammonite subfamily Labeceratinae Spath, 1925, is a small group of heteromorphs, restricted to the Upper Albian, and generally assumed to be south Gondwanid or Austral in distribution (Collignon 1932: 25; Venzo 1936: 124; Collignon 1950: 84; Wiedmann 1965: 443; Kennedy 1972: 402; Förster 1975: 173; 1981: 168; Klinger 1976: 37; McNamara 1978: 240). The size of the group, conspicuous morphology, and short temporal and limited geographical occurrence is ideal for studying some identifiable factors that may have influenced the palaeobiogeographical distribution.

SYSTEMATICS, PHYLOGENY AND DIMORPHISM

Taking Wright's (1957: L231–L232) classification as a starting point, the systematics of the group may be discussed.

Superfamily SCAPHITACEAE Meek, 1876

Family **Labeceratidae** Spath, 1925

(= Aleteceratidae Whitehouse, 1926; Myloceratidae Spath, 1939)

Genus *Labeceras* Spath, 1925

Subgenus *Labeceras* (*Labeceras*) Spath, 1925

Subgenus *Labeceras* (*Appurdiceras*) Whitehouse, 1926

Genus *Myloceras* Spath, 1925

Genus *Ellipsoceras* Collignon, 1950

(= *Abadieceras* Collignon, 1950)

? Genus *Hamitoides* Spath, 1925

This classification was based mainly on ideas of Spath (1925: 191, *et seq.*; 1930: 57; 1939: 600–601), many of which no longer hold true or need updating. The alleged scaphitoid affinity of the subfamily as advocated by Spath (1925: 191; 1939: 601), and followed by Wright (1957: L231) and Luppov & Druschits (1958: 125), was based on superficial homoeomorphy and incorrect interpretation of sutural data. It was questioned by Schindewolf (1961: 109) and convincingly disproved by Wiedmann (1962: 84; 1965: 443) and Wiedmann & Dieni (1968: 74), who would rather place the group in the family Anisoceratidae, a view followed by Reyment (1964b: 37), Klinger (1976: 36) and McNamara (1978: 232). But, as Förster (1975: 172) has pointed out, the trifid lobes are more like those of Ancyloceratinae rather than Anisoceratidae with predominantly bifid lobes. However, the stratigraphic gap between the last occurrence of Ancyloceratinae at the top of the Lower Albian, and the first occurrence of Labeceratinae at the base of the Upper Albian has to be bridged.

I previously (Klinger 1976: 41, pl. 12 (figs 3–4, 6), text-figs 7i–j, 8a), recorded *Labeceras* sp. nov. aff. *L. crassicoatum* from the third, possibly fourth, division of the Albian of Zululand. Additional material (Fig. 1) has since been found that suggests the presence of an as yet unnamed heteromorph with labeceratid coiling and simple sharp ribbing, and another with apparent crioceratid coiling and ventrally tuberculate fine ribbing. The sutures have asymmetrically trifid lobes L, U and I. It would be tempting to regard these as the connecting link between the last Ancyloceratinae and the first Labeceratinae, as envisaged by Förster (1975: 172). However, apart from the suture lines, the regular tuberculation, style of ribbing and planispiral coiling are very difficult to reconcile with the first true Labeceratinae in the Upper Albian of Zululand, and I would rather regard them as homoeomorphic, but ancestrally distinct, hamitids or anisoceratids. Similar faunas were described from the Middle Albian of the Samana Range of India by Spath (1930) and are worth reinvestigating.

In Zululand, the first forms definitely identifiable with *Labeceras* and *Myloceras*, *Labeceras crassetuberculatum* Klinger, 1976 (Fig. 2) and *Myloceras*

rotundum Klinger, 1976 (Figs 3C–E, 4), occur in the lower part of the fifth division of the Albian. Next, *Labeceras plasticum* Spath, 1925 (Fig. 3A) *Myloceras serotinum* Spath, 1925 (Figs 5–6), and *M. cornucopia* Spath, 1925, are common. This association is followed by common *Labeceras inflatum* Förster 1975 (= *Labeceras ovale* Klinger, 1976) (Fig. 7B), *L. rectum* Klinger, 1976 (Fig. 3B), and *Myloceras besairiei* Collignon, 1932. Rare elements in the latter association also include *Ellipsoceras expansum* Collignon, 1950. This is slightly oversimplified (cf. Klinger 1976) but several distinct morphological trends can be observed (Fig. 8). These are from oldest to youngest.

Labeceras

1. Decrease in overall size.
2. Lateral lobe (L) changes from asymmetric to symmetrically trifid.
3. Whorl section becomes more compressed.
4. Coiling initially typically labecera-tid, with curved shaft and inward-facing aperture. Later forms with straight shaft, aperture parallel to shaft, very similar or identical to *Myloceras*, and can only be distinguished by virtue of the lateral tubercles.
5. Ornament becomes subdued in later forms and umbilical tubercles reduced.

Myloceras

1. Decrease in overall size.
2. Lateral lobe (L) changes from asymmetric to symmetrically trifid.
3. Whorl section becomes more compressed.
4. Coiling on criocone whorls becomes more regular and compact; distinct change in whorl section near point of uncoiling. Shaft possibly tends to recurve in *Ellipsoceras*.
5. Ornament initially very irregular with variable number of minor to major and/or tuberculate to non-tuberculate ribs. Ribbing later more regular and tending to become more uniform.

Given the range of diversity and also overlap of coiling in Labeceratinae, I doubt if *Ellipsoceras* deserves separate generic rank. Apart from the curious coiling, which has so far been observed only in the holotype of *Ellipsoceras expansum* (Collignon, 1950, pl. 14(5) (fig. 2)), *Ellipsoceras* has ornament of the type of *M. besairiei* Collignon, and is here included in the synonymy of *Myloceras*.

Against this background it is now possible to look at the systematic position of the poorly known genus *Hamitoides* Spath, 1925, which had in the past either been referred to the Labeceratinae with doubt (Spath 1925: 191; 1930: 57; 1939: 600; Wright 1957: L232; Klinger 1976: 36–37) or was considered to be a link between *Hamites* and *Labeceras* (Spath 1925: 191; 1939: 601; Haas 1942: 187; Wiedmann 1962: 98; Wiedmann & Dieni 1968: 74).

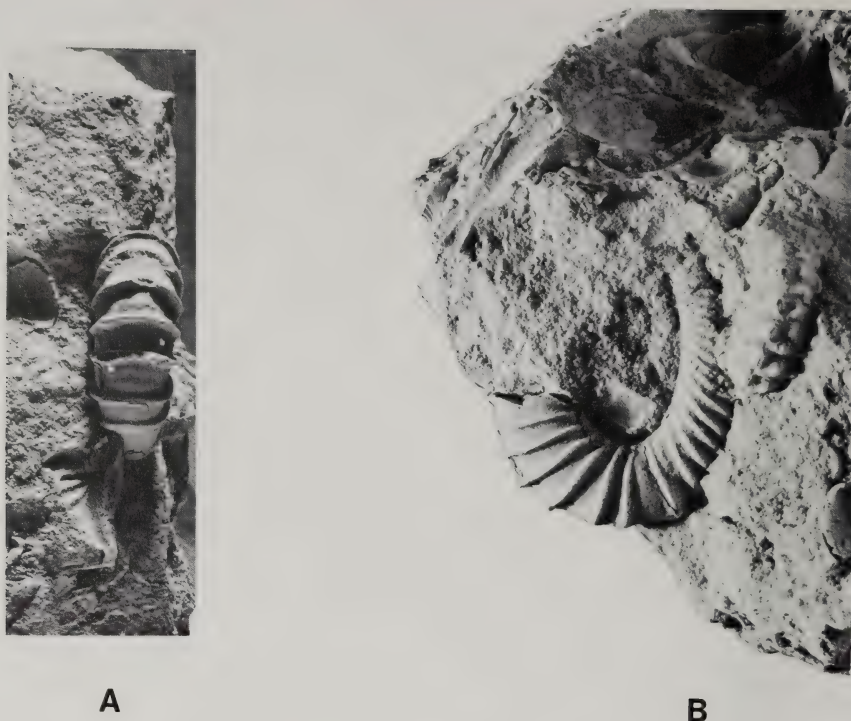


Fig. 1. Gen. et. sp. indet (*Hamites?*), SAM-KK154. Material previously described by Klinger (1976: 41, pl. 12 (figs 3–4, 6), text-figs 7i–j, 8a) as *Labeceras* sp. nov. aff. *L. crassicostatum* from Albian III–IV? Note association with *Lyelliceras lyelli*. $\times 1$.

The type species of *Hamitoides*, *H. studerianus* as interpreted in terms of the lectotype of the species (in Pictet 1847, pl. 15 (fig. 1)), is certainly not a labeceratid. The straight shaft and rounded whorl section are combinations as yet unknown in Labeceratinae, especially in view of the fact that the type material ranges from the Middle Albian to the lower Upper Albian.

Several alleged *Hamitoides* have been recorded from the Middle Albian of Madagascar: *Hamitoides?* *madagascariensis* Breistroffer (1936: 174, pl. 20 (figs 6–9, fig. 10i); Collignon 1963: 45, pl. 258 (figs 114–115)), *Hamites studeri* (Collignon, 1932: 22, pl. 4 (figs 10–13)), *Hamitoides* aff. *studer* (Collignon 1963: 43–45, pl. 257 (figs 1110–1111), pl. 258 (fig. 1116)).

The specimens referred to the type species by Collignon (1963) may, according to Wiedmann & Dieni (1968: 74), possibly belong to *Eoscaphtes tenuicostatus* (Pervinquière) and not involve Labeceratinae at all. *Hamitoides madagascariensis* is too poorly known for definite comment.

Venzo (1936: 111 (53)) recorded two specimens from Zululand as *Hamites studeri*. These are misidentified shafts of *Labeceras plasticum*. *Hamitoides* sp.

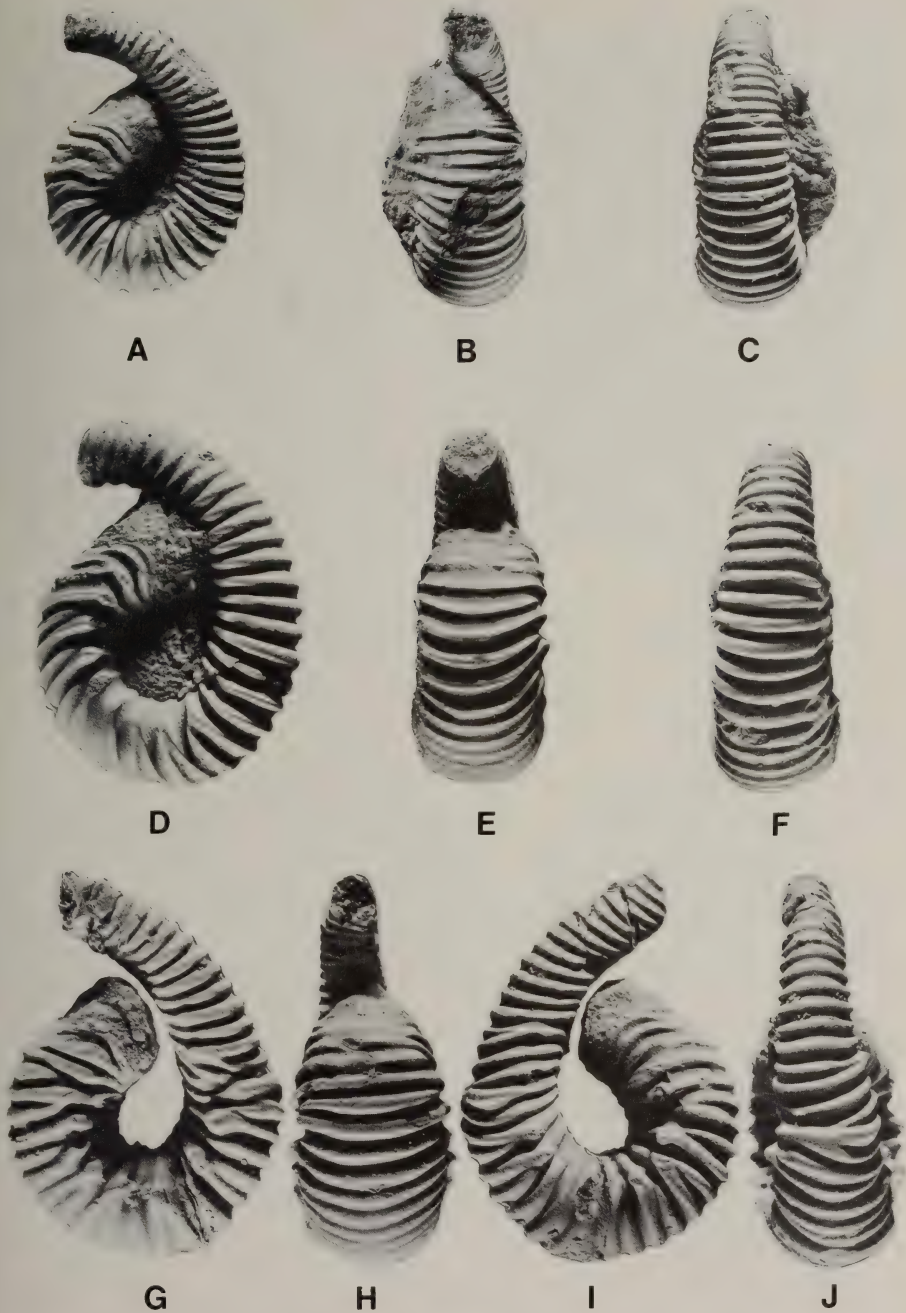


Fig. 2. *Labecerat crassetuberculatum* Klinger, 1976. A-C. NMB-D578.
D-F. SAM-PCZ205/5/7/, the holotype. G-J. NMB-D2372.
All $\times 1$.

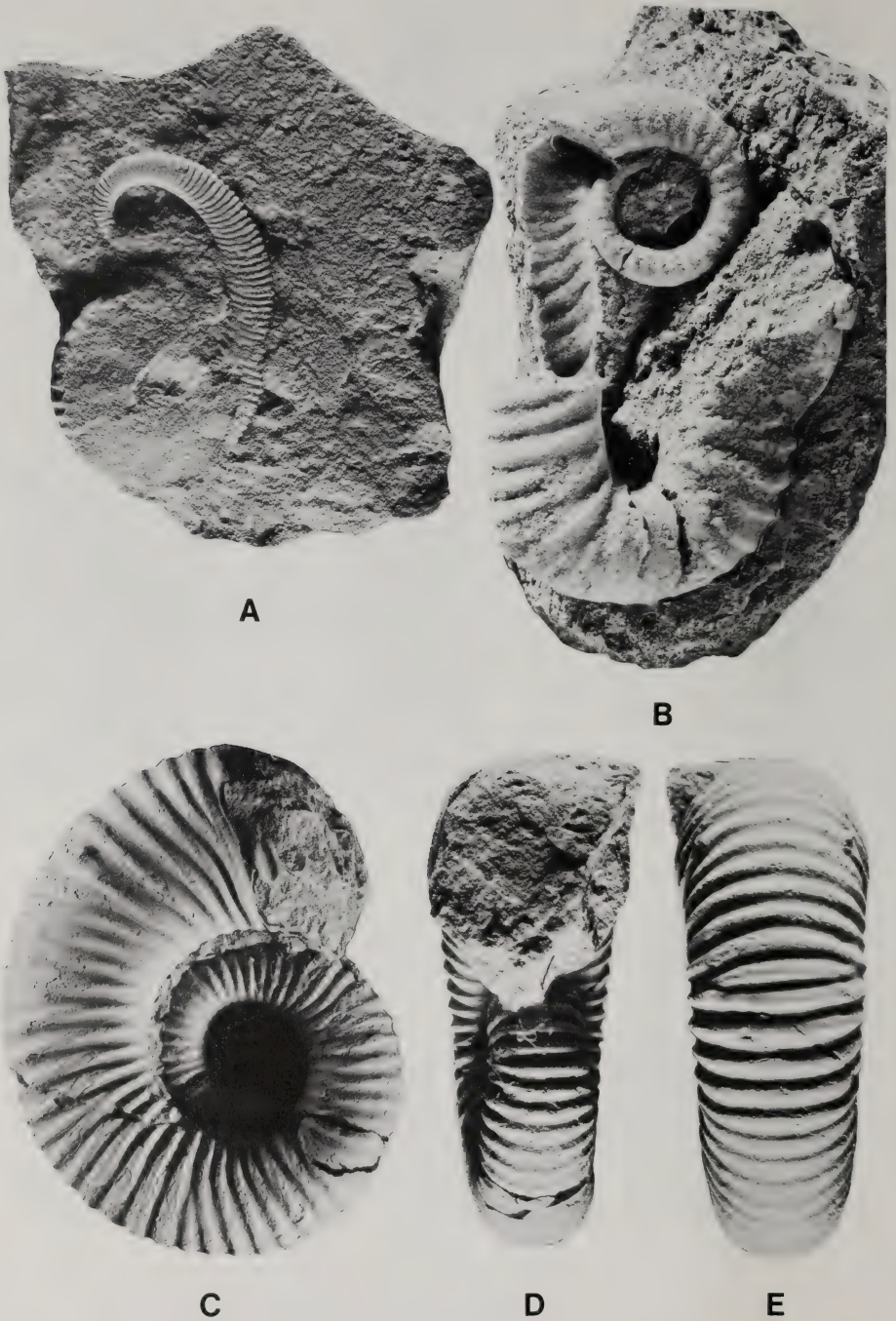


Fig. 3. A. *Labecerases plasticum* Spath, 1925. SAS-EM127. $\times 1$. B. *Labecerases rectum* Klinger, 1976. NMB-D736. $\times 2$. C-E. *Myloceras rotundum* Klinger, 1976. NMB-D496. $\times 1$.

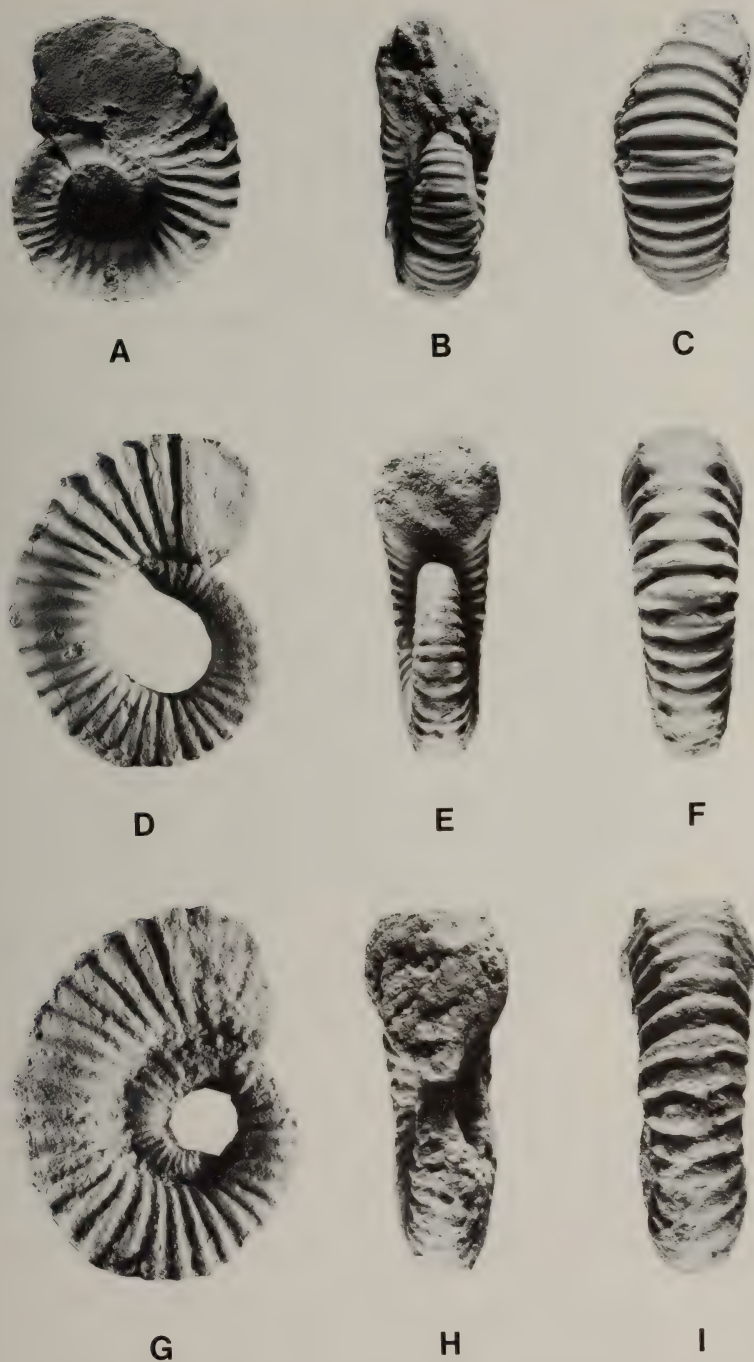


Fig. 4. *Myloceras rotundum* Klinger, 1976. A-C. NMB-D429. D-F. NMB-D294a. G-I. NMB-D294b. All $\times 1$.

ind. from the Samana Range of India (Spath 1930: 62) was neither figured nor described and I cannot comment on it.

Hamitoides angolanus Haas (1942: 187, pl. 45 (fig. 3a–e), text-figs 28a–b) is from the Upper Albian of Hanha, Angola. The holotype consists of a recurved hook and part of the shaft. It is wholly septate, thus definitely excluding labeceratine affinities—rather suggesting ptychoceratid affinities. Thus interpreted, *Hamitoides* definitely does not belong in the Labeceratinae.

McNamara (1980: 147) has recently shown that the type species of *Labeceras* (*Appurdiceras*) Whitehouse, 1926—*Ancyloceras corcyceoides* Etheridge (1905: 14, pl. 1 (figs 3–5), pl. 2 (fig. 4)), is in fact an anisoceratid and should be removed from Labeceratinae. The subfamily Labeceratinae is thus effectively reduced to the two genera, *Labeceras* and *Myloceras*.

Below generic rank, systematics of the Labeceratinae becomes difficult, due to the low specific diversity but extreme intraspecific variation. However, one of the most consistent features of labeceratid systematics is the consistent association of *Labeceras* and *Myloceras* (e.g. McNamara 1978: 241) throughout the known stratigraphic range of the group.

Distinct successive pairs of *Labeceras* and *Myloceras* can be recognized. In both there seems to be an increasing trend towards hydrodynamic stability and/or 'streamlining' of ornament. This leads to surprising homoeomorphy between *Labeceras* and *Myloceras* (Fig. 7).

This raises the question of dimorphism in Labeceratinae—i.e. whether *Myloceras* is the macroconch and *Labeceras* the microconch.

Apart from the scaphitids (see e.g. Makowski 1963; Cobban 1969), dimorphism has only recently been recognized in heteromorph ammonites and remains largely to be explored in Cretaceous groups (see Callomon 1981: 267).

Distinct dimorphism has been recognized in the baculitid genera *Sciponoceras* (Marcinowski 1980: 253; see also Kennedy & Juignet 1983: 17), *Lechites* (Cooper & Kennedy 1977), *Baculites* (Kennedy 1984: 143—in *Baculites incurvatus*; Klinger & Kennedy in prep.—in *Baculites capensis*), and in the heteroceratine species *Colchidites vulanensis* (Aguirre Urreta & Klinger 1986: 350). It has also been suggested for several other groups, e.g. *Bostrychoceras* (Kennedy 1986: 95), *Eubostrychoceras* (Kennedy 1986: 101), *Hamites* (Cooper, unpublished data; Kennedy & Juignet 1983: 12), *Tridenticeras* (Kennedy 1984: 138), and '*Neancyloceras*' (Klinger 1982: 229).

In most of these groups, dimorphism manifests itself mainly by differences in size and, where preserved, in apertural modifications. This would correspond more or less to Type II dimorphism of Houša (1965), where the sexes differ not only in size, but where the male has apertural outgrowths, such as lateral lappets or a ventral rostrum.

Dimorphism has previously been suggested for Labeceratinae but, in my opinion, for the wrong reasons. Spath (1925: 192) suggested that forms with and those without croziers (in *Myloceras*) might be dimorphs. This would be a situation analogous to that found in *Macroscaphites* and *Costidiscus*, as suggested by

**A**

Fig. 5. *Myloceras serotinum* Spath, 1925. SAS-Z174. $\times 1$.

Callomon (1981: 267). However, the Zululand material does not support this view.

Förster (1975: 176) suggested that *L. plasticum crassum*, which consists of predominantly large, inflated, strongly tuberculate forms, may differ from the generally smaller and more weakly tuberculate *L. plasticum plasticum* on account of sexual dimorphism. By analogy with the scaphitids (e.g. Makowski 1963: 31, *et seq.*; Cobban 1969), this is the situation one would expect in *Labe-ceras*. Also, by analogy with the scaphitids, we would expect the range in size to



Fig. 6. *Myloceras serotinum* Spath, 1925. A-B. SAS-Z174. $\times 1$.

be such that the largest microconchs would be larger than the smallest macroconch, but not as large as the largest macroconch. In the available material we find that the coarsely ornamented forms are generally larger than the more finely ornamented forms, but that the size overlap of these forms is virtually 1:1. Size distribution patterns of *L. crassetuberculatum*, *L. plasticum*, *L. rectum* and *Myloceras serotinum* are shown in Figure 9. Apertural lappets are generally taken to be characteristic of micromorphs. Spath (1925: 192, pl. 31 (fig. 4b-c)) noticed that in *Labceras plasticum* 'The aperture is provided with a short dorsal

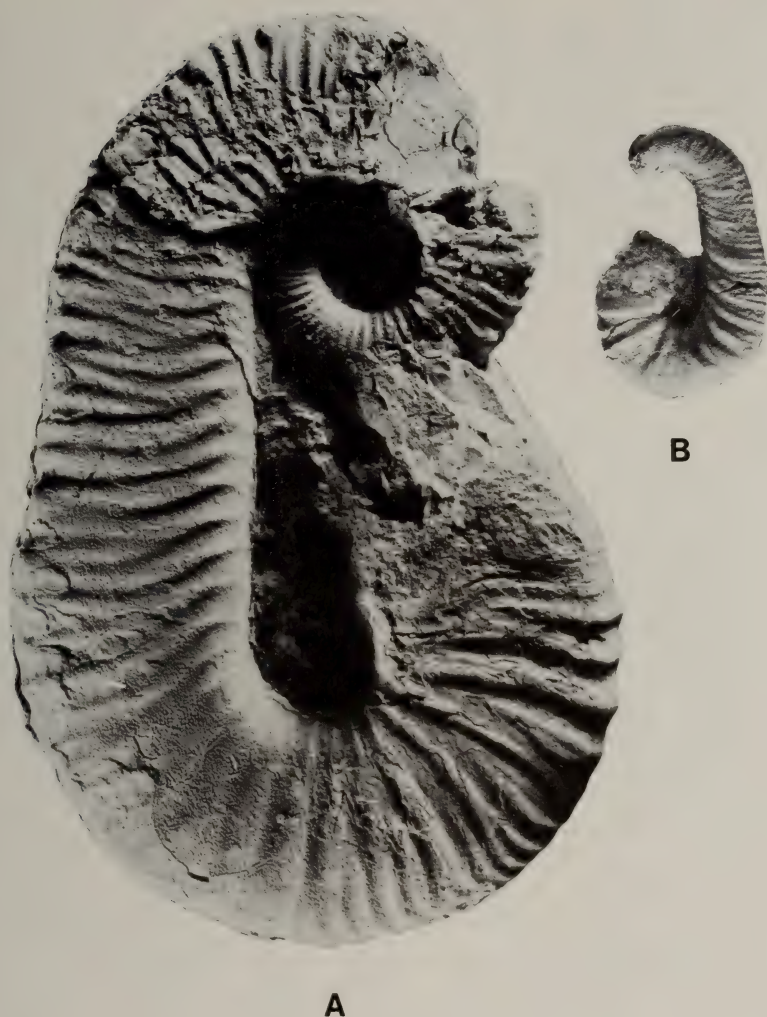


Fig. 7. A. *Myloceras serotinum* Spath, 1925. SAM-PCZ7665. B. *Labeceras inflatum* Förster, 1975. NMB-D2702. Both $\times 1$. Note homoeomorphy between *Labeceras* and *Myloceras* suggesting dimorphism.

and two longer lateral lappets' and in *Myloceras serotinum* (1925: 193, pl. 33 (fig. 1)) 'The aperture, as restored . . . shows a slight ventral and two more prominent lateral lappets'. Subsequently Wright (1953: 473) noted that '... *Labeceras* has lateral lappets, whereas the probably closely related *Myloceras* has an aperture merely with a sinuous border'.

Material from Zululand shows that lateral lappets occur in both *Labeceras* and *Myloceras* but, that in relation to overall shell size, those of *Labeceras* are much larger than those of *Myloceras* (Figs 13–15).

Thus, unless we are dealing with isochronous parallelism or homoeomorphy, it seems plausible to regard *Labeceras* and *Myloceras* as a dimorphic pair—the former being the microconch, the latter the macroconch.

I admit that this may appear as an extreme form of dimorphism not previously recorded in other heteromorph groups. It would be ideal to show that the nuclei of *Labeceras* and *Myloceras* are identical, thus lending further credibility to the assumption that they are dimorphs. Unfortunately nuclei are not available and, at the smallest diameters preserved, *Myloceras* is distinctly tuberculate and *Labeceras* non-tuberculate. However, if they are indeed dimorphs, the comparisons proposed by Förster (1975: 172–173) between *Myloceras* and *Australiceras*, and *Labeceras* and *Toxoceratoides*, may not be as preposterous as they seem—although the taxonomic implications are frightening.

This systematic arrangement of the subfamily Labeceratinae seems far removed from that adopted by Wright (1957: L231–L232) but, in the light of current data and from a phylogenetic point of view, makes much more sense. This effectively reduces the subfamily Labeceratinae to one dimorphic genus. Until details of the complex synonymies have been worked out, I prefer to retain both generic names *Labeceras* and *Myloceras* in this discussion, albeit mainly for the sake of taxonomic 'neatness'.

Within this systematic framework it is now possible to look at the stratigraphic and geographic distribution of the subfamily Labeceratinae.

DISTRIBUTION

Records of *Labeceras* from the Albian of England (Owen 1971: 195) are based on misidentifications of a labeceratid homoeomorph, *Idiohamites ellipticoides* Spath, 1939 (see Kennedy 1972: 400–404). All other records of Labeceratinae are of Gondwanid origin (Fig. 10). These include:

1. *Australia*. Occurrences here are in the Great Artesian Basin of Queensland and in South Australia (see Ludbrook 1966 for summary). Individual references include McCoy (1867), Etheridge (1909—South Central Queensland), Whitehouse (1926—South Central Queensland), Reyment (1964a, 1964b—South Australia), and McNamara (1978—Central Queensland).

Precise data are not available, but the *Myloceras*–*Labeceras* assemblages have been dated as middle Late Albian (McNamara 1978: 231), or as being equivalent to the *varicosum*–*aequatoriale* subzones of the Gault of England (Spath 1925: 194) or possibly the *orbigny* subzone (Whitehouse 1926: 197; also Reyment 1964a: 34).

2. *New Guinea*. Glaessner (1958: 217–218) recorded *Myloceras davidi* Whitehouse, *Myloceras* cf. *flindersi* (McCoy), and *Labeceras trifidum* Whitehouse from the Albian of New Guinea.

3. *New Zealand?* Wellman (1959: 121) and Henderson (1973: 99) recorded a single questionable fragment of *Myloceras* from the Clarence Series at Wairarapa on North Island.

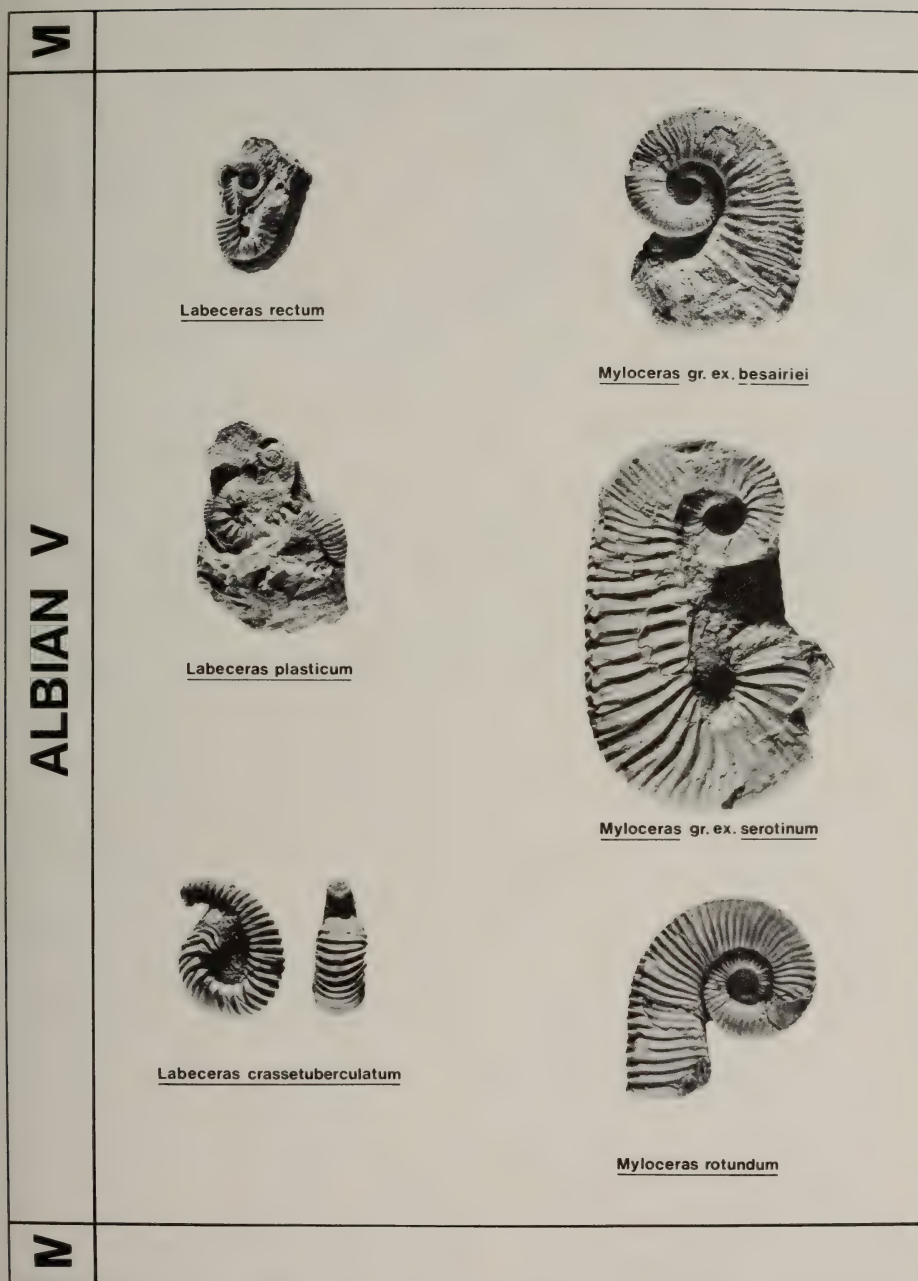


Fig. 8. Suggested phylogenetic sequence of *Labeceras* and *Myloceras* in Zululand. All reduced by various fractions to fit diagram.

4. *Antarctica*? Thomson (1984: 89) mentioned small heteromorphs 'possibly *Labeceras*' from the Albian of Lost Valley on James Ross Island in Lesser Antarctica.

5. *Somalia*? Tavani (1942: 30 (116), pl. 3 (pl. 12) (fig. 8)) recorded a single specimen from the Albian of Sceec Gure (Bugda Acable), Somalia, as *Labeceras plasticum*. The specimen is very poorly preserved but the presence of straight, near-parallel shafts seems to indicate '*Hamitoides*' rather than *Labeceras plasticum* affinities.

6. *Madagascar*. A very well-documented labeceratine fauna is known from Madagascar. Individual references include Boule *et al.* (1907—Andrakaka, Diego-Suarez), Besairié (1932), Collignon (1932—Mont Raynaud), Collignon (1936—Maniamba-amba), Collignon (1950—Mokaraha), Collignon (1951—Andranofotsy, Manja), Collignon (1963—Diego-Suarez, Betioky (Vohimaranitra), Andronofotsy (Manja), Mokaraha (Soalala)), and Besairié & Collignon (1972).

This fauna is well dated and, according to the biozonation compiled for Madagascar by Collignon (1963), ranges from the lowermost zone of the Upper Albian, Zone à *Dipoloceras cristatum*, through the Zone à *Hysterocheras binum* to the penultimate Zone à *Pervinquieria inflata*.

The systematic position of *Euhemihoplites paradoxus* Collignon (1964: 38, pl. 326 (fig. 1457)), reported from the Lower Cenomanian, Zone à *Mantelliceris mantelli* et *Calycceras newboldi*, should be mentioned here. According to

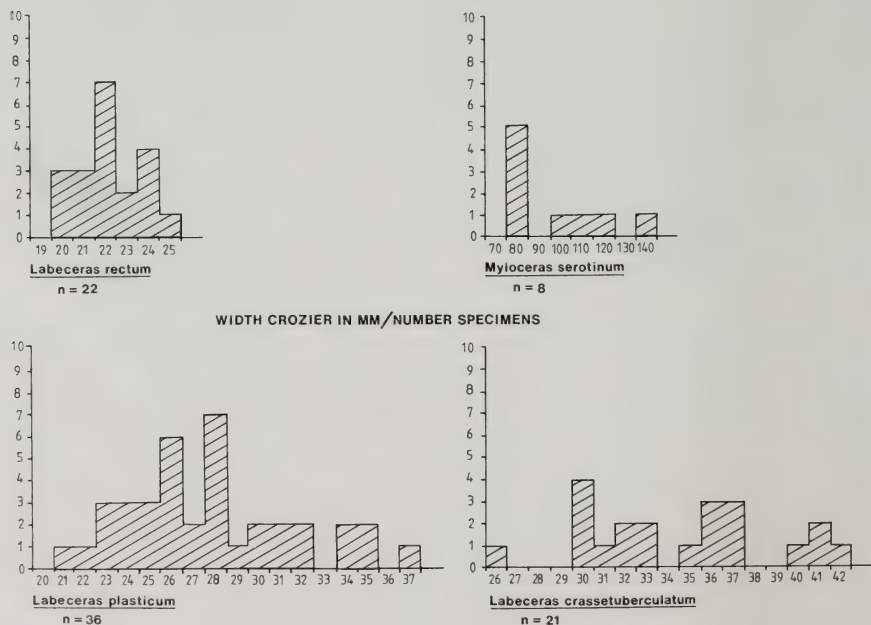


Fig. 9. Size distribution in *Labeceras* and *Myloceras*.

Kennedy (1985), this species, based on a single fragment, may in fact be a *Myloceras*, probably derived from Upper Albian strata. It is similar to a new species described below in possessing umbilical tubercles.

7. *Mozambique*. The original labeceratid material on which Spath's (1925: 191, *et seq.*) descriptions were based, are probably from near Catuane in southern Mozambique—Förster's (1975: 32) locality Lagoa Catuine. Other localities yielding labeceratids include Rio Zepundune, Road Metal Quarry 9,5 km north of Catuane, Rio Comane, and Rio Changalane.

The stratigraphic range of labeceratids in southern Mozambique was compared to the standard European succession of *varicosum* to *aequatoriale* subzones of the *Mortoniceras inflatum* Zone.

8. *Zululand*. Labeceratids are locally very common in Kennedy & Klinger's (1975: 276) fifth division of the Albian. References include Besairié (1930: 622—Mzinene), Venzo (1936: 113 (55), *et seq.*—Ndabana-Mzinene), Kennedy & Klinger (1975: 276), Klinger (1976: 36, *et seq.*—Mzinene River, Ndambana Creek, Ndumu, Mkuze Game Reserve, Munywana River), and Haughton (1936: 292—Pongola River).

Definite *Labeceras* and *Myloceras* first occur in the fifth division of the Albian in association with *Dipoloceras cristatum*, '*Deiradoceras*', '*Drepanoceras*' and '*Rhytidoceras*'. Later forms of the group *Myloceras besairiei*, with extremely compressed whorl section and regular ornament, and *Labeceras rectum* occur in association with *Pervinqueria* (P.) and *P. (Styphloceras)*. In comparison with



Fig. 10. Palaeobiogeographic distribution of *Labeceras* and *Myloceras*. Map based after Smith & Briden (1973).

Madagascar, this would suggest a definite range of Upper Albian, Zone à *Dipoloceras cristatum* to Zone à *Pervinquieria inflata*.

9. *Argentina* (Patagonia). Leanza (1970: 202, 209) recorded two new genera, *Calliscaphites*, type species *Calliscaphites andinus* Leanza, 1970, and *Paraleptoceras*, type species *Paraleptoceras singulare* Leanza, 1970, from the Albian of Estancia La Vega, in the Santa Cruz Province of Patagonia. These are clearly synonyms of *Myloceras* Spath and *Labeceras* Spath and, from the limited figured material available, seem close to *Myloceras rotundum* Klinger and *Labeceras crassetuberculatum* Klinger.*

Subsequent reports from the Santa Cruz Province include Nullo *et al.* (1981, pl. 2 (fig. 10—*Labeceras?* sp., fig. 11—*Calliscaphites andinus*)) and Riccardi & Rollieri (1980: 1198).

Medina & Rinaldi (1986) recorded both *Myloceras* and *Labeceras* from Estancia La Vega in Santa Cruz Province, as do Riccardi *et al.* 1988. Unfortunately, this is the only known locality in the Austral Basin with labeceratids and, in addition, the outcrop is rather small.

BIOGEOGRAPHIC AND STRATIGRAPHIC IMPLICATIONS

Distribution of the Labeceratinae is strictly Gondwanid—more specifically south Gondwanid. Two features are conspicuous:

1. Concentration of Labeceratinae into two main regions—south-eastern Africa–Madagascar and Australia.
2. Conspicuous absence of Labeceratinae in India and, with the exception of the Austral Basin of Patagonia, absence in the South Atlantic.

South-eastern Africa–Madagascar and Australia

Correlation of Labeceratinae faunas between south-eastern Africa–Madagascar and Australia is tenuous, mainly due to a combination of taphonomy, differential preservation and systematics. Complete specimens of *Myloceras* and *Labeceras* are rare, and most descriptions are based on incomplete material.

To this must be added the effects of disparate sizes and intraspecific variation. Some of the Australian species of *Myloceras* are gigantic, e.g. *Myloceras axononoides* (Etheridge, 1909, pl. 44 (fig. 2)) and *Myloceras nautiloides* (Etheridge, 1909, pl. 45), and no Afro–Malagassy specimens are known that even approximate the Australian giants in size (Figs 11–12).

It is difficult to evaluate the reports of species common to both areas (e.g. Venzo 1936: 55 (113); Reyment 1964a: 23; Förster 1975: 176; Klinger 1976). From these records it appears that the only species probably common to south-eastern Africa–Madagascar and Australia, are *Labeceras bryani* Whitehouse and *L. plasticum* Spath.

Out of a total of about 40 described species, this is indeed a very low correlation factor. However, even given the effects of intraspecific variation, analysis of the faunas still shows some differences.

* See p. 219 for note added at proof stage.

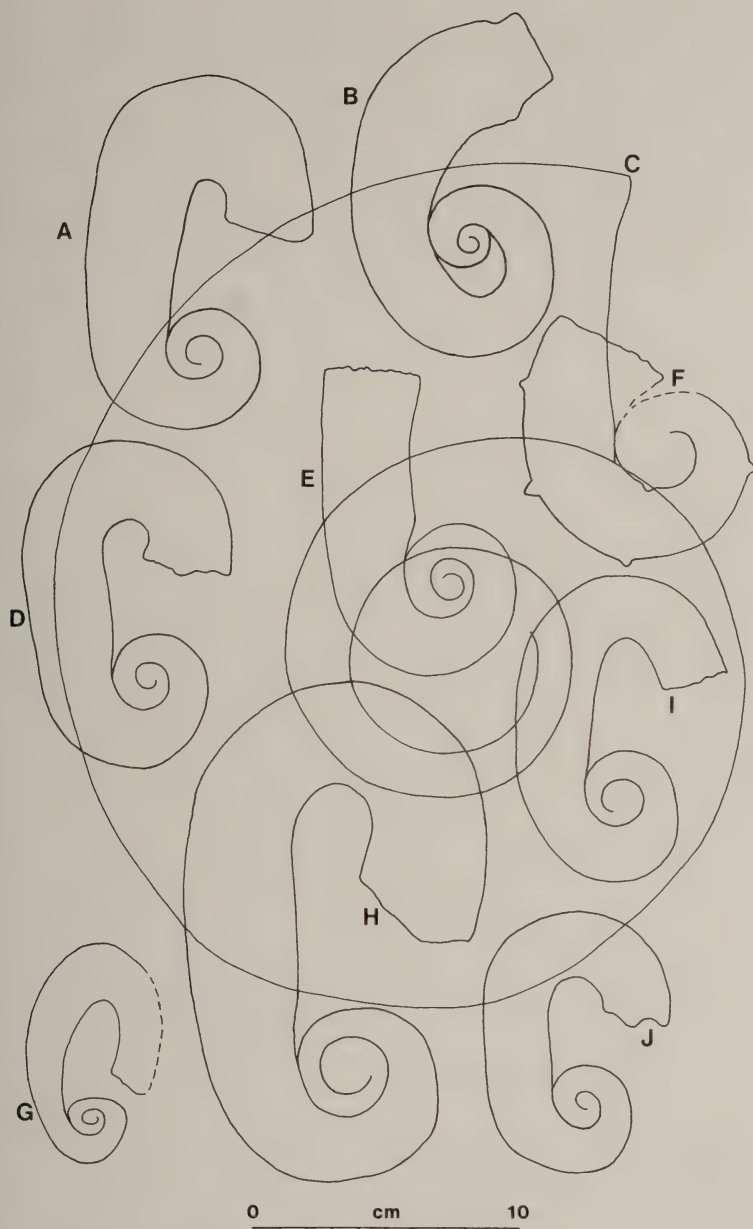


Fig. 11. Variation in size in *Myloceras*. A. *Myloceras serotinum* Spath, 1925. SAS-Z174. B. '*Ellipsoceras*' *expansum* Collignon, 1950. Holotype. C. *M. axonoides* Etheridge, 1909. Holotype. Half size compared to other specimens. D. *M. serotinum* Spath, 1925. SAM-7665. E. *M. cornucopia* Spath, 1925. Holotype. F. *M. amalthia* Spath, 1925. Holotype. G. *M. mokaharensis* Collignon, 1964. Holotype. H. *M. auritulum* McNamara, 1978. Holotype. I. *M. serotinum rugosa* Spath, 1925. Holotype. J. *M. serotinum* Spath, 1925.

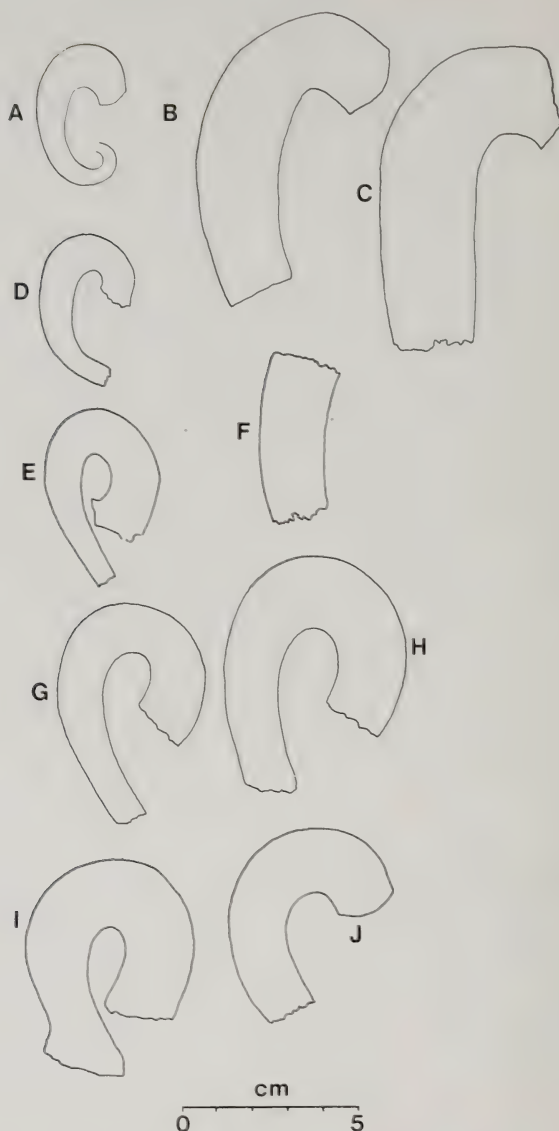


Fig. 12. Variation in size in *Labecerases* (and one specimen of *Myloceras*). A. *L. plasticum* Spath, 1925, the holotype. B. *L. gracilis* Collignon (1964, fig. 1140). C. *Myloceras serotinum elliptica* Collignon (1965, fig. 1137). D. *L. plasticum crassa* Spath, 1925, the holotype. E. *L. etheridgei* Whitehouse, 1926 (pl. 38 (fig. 2)). F. *L. plasticum* (Collignon, 1964, fig. 1125). G. *L. papulatum* Whitehouse (1926, pl. 39 (fig. 3)). H. *L. hourcqi* Collignon (1950, pl. 14 (fig. 1)). I. *L. compressum* Whitehouse, 1926 (1950, pl. 39 (fig. 5)). J. *L. crassicostatum* Collignon, 1950 (pl. 13 (fig. 5)).

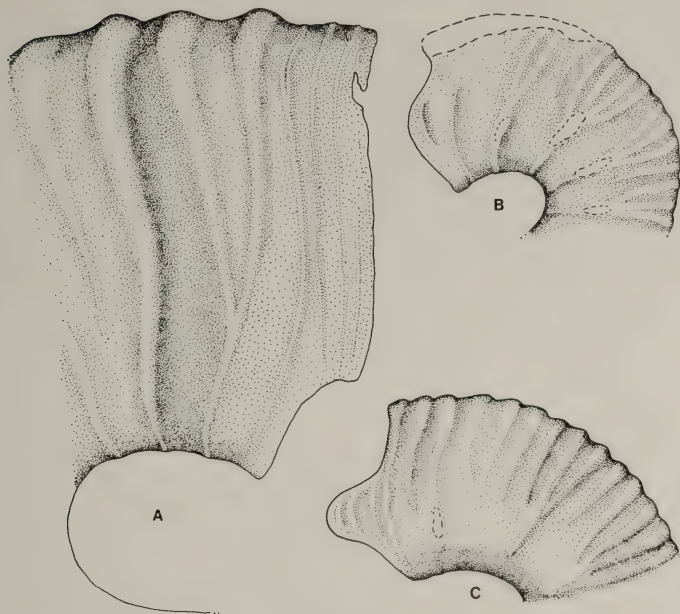


Fig. 13. A. Sketch of aperture of *Myloceras serotinum*. SAM-7665. $\times 3,9$.
B-C. *Labeceras plasticum*. B. SAM-Z450. C. A2173.

The only reliable feature in the systematics of *Myloceras* appears to be the whorl section (see also Reyment 1964a: 31). Taking the phylogenetic sequence (Fig. 8) as a basis for comparison, three groups can be recognized: *Myloceras* gr. ex. *rotundum* with round to reniform whorl section, *Myloceras* gr. ex. *serotinum* with rectangular depressed to compressed whorl section, and *Myloceras* gr. ex. *besairiei* with rectangular to very compressed whorl section. A similar crude analysis can be done on *Labeceras*, based on the nature of the shaft—*Labeceras* gr. ex. *crassetuberculatum* with incurved, asymmetrically coiled shaft, *Labeceras* gr. ex. *plasticum* with distinctly curved shaft, and *Labeceras* gr. ex. *rectum* with straight shaft and very often a distinct nick-point and coiling, virtually as in *Myloceras*.

Within this crude framework Australian and Afro-Malagassy forms can be compared. No forms similar to *Myloceras* gr. ex. *besairiei* or *Labeceras* gr. ex. *rectum* are known from Australia, i.e. comparisons are possible amongst stratigraphic early forms but not amongst the later, established ones.

Though fully aware of the possible errors in the systematics of the subfamily, the above data do point to significant differences between the Australian and Afro-Malagassy faunas, and seem to suggest considerable endemism in the two labeceratine populations, especially as far as the apparent phylogenetically more advanced forms are concerned. This also implies restricted necroplanktonic

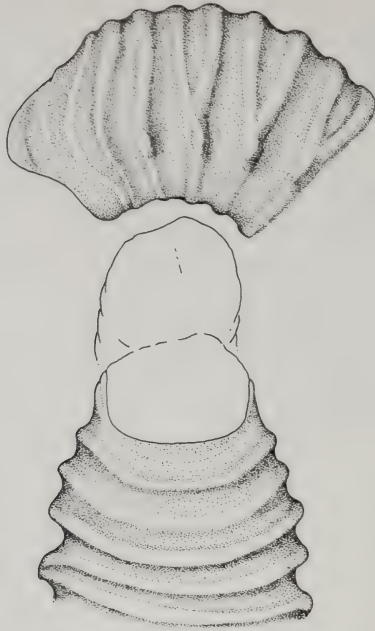


Fig. 14. Sketch of aperture of *Labceras crassetuberculatum*. EM 151. $\times 3.9$.

dispersal in at least part of the population, which is at variance with the views held by Reyment (1964a: 33).

India

Data on the Cretaceous of southern India mainly date back to Forbes (1846), Stoliczka (1863–1865), and Kossmat (1895–1898). The most recent stratigraphic syntheses of the Cretaceous of southern India are by Sastry *et al.* (1968) and Gupta (1975). The lowermost Utatur Group is a mixture of Upper Albian and Cenomanian. The lower *Schloenbachia inflata* Zone contains a mixture of Upper Albian and Lower Cenomanian faunas. According to Spath (1925: 196) the sequence only starts with the *aequatoriale* subzone, i.e. the uppermost part of the European *inflatum* zone. Thus, on stratigraphic data alone, chances of finding Labeceratinae in southern India are very slender. New collections being studied by Dr M. A. Ghare (letter 17.7.84) contain numerous new records of heteromorph genera, but no labeceratines.

South Atlantic

Apart from one locality, Estancia La Vega, in the Austral Basin of southern Patagonia, no Labeceratinae are known from the South Atlantic.

The stratigraphic range of the Labeceratinae coincides with part of the opening-up of the South Atlantic Ocean. For discussions see e.g. Beurlen

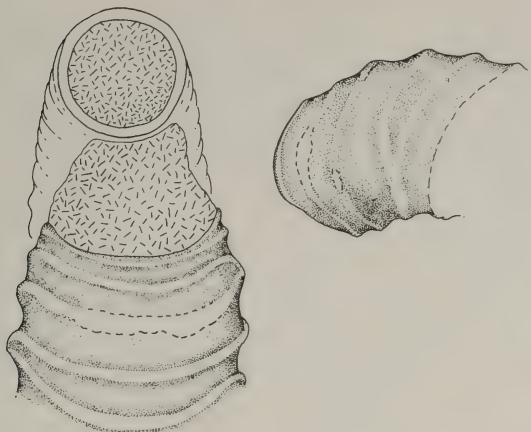


Fig. 15. Sketch of aperture of *Labecerat crassetuberculatum*.
H207/5/7. $\times 3.9$.

(1961), Reyment & Tait (1972), Van Andel *et al.* (1977), Sclater *et al.* (1977), Melguen *et al.* (1979), Reyment (1980), Rand & Mabesoone (1983), etc. It is possible that the distribution of the group may have been influenced in part by these circumstances (Fig. 16).

Whatever the exact dates of North and South Atlantic marine connections may be, it seems reasonable to accept that surface currents existed (Berggren & Hollister 1974; Lloyd 1982) and that free faunal migration was possible between south-eastern Africa–Madagascar, via the Cape Sea Route, through the Atlantic, as far north as the Venezuelan Andes, Mexico and Texas during the Upper Albian (e.g. Kennedy & Cooper 1975: 284–285; Kennedy & Cobban 1976: 77; Förster 1978: 158; 1981: 167–168; Renz 1981: 201; 1982).

Absence of records of Labeceratinae from the Cape Basin is due to the absence of onshore exposures. No onshore Albian exposures are known between southern Angola and Zululand, a distance of some 3 500 km. Offshore drilling on the Orange River delta may hold some prospects. However, the absence of Labeceratinae from the Upper Albian of the Brazil–Angola Basin seems real, and not due to collecting failure, non-exposure of relevant strata or misidentifications, as various extensive faunal lists from this region seem to substantiate, e.g. Spath (1922), Haas (1942), Howarth (1965), Reyment (1955, 1956, 1978, 1981), Cooper (1978), Collignon (1978), and Cooper & Kennedy (1979).

Prevailing conditions in the Upper Albian in the Brazil–Angola Basin seem to have been favourable for development of endemic faunas, e.g. the mortoniceratine genus *Elobiceras* (e.g. Reyment 1981: 149), but unfavourable for the entry of others, e.g. the Labeceratinae, while apparently having no effect on others.



Fig. 16. Palaeo-reconstruction of opening of the Atlantic Ocean. Map based mainly on Dingle *et al.* 1983.

There seems to be little consensus on the physical size and effect of the Walvis Ridge separating the Angola Basin from the Cape Basin, ranging from a submerged chain to a series of islands (e.g. various references in Sclater *et al.* 1977; Bolli *et al.* 1978; Reyment 1980; Rage 1981), nor on its effects on the distribution of invertebrate faunas (e.g. Scheibnerová 1978, 1981; Tambareau 1982; Dingle 1984). However, as the South Atlantic progressively opened, circulation in the Cape Basin seems to have kept one step ahead of that of the Angola Basin, especially after the Falkland Plateau had cleared the tip of Africa at about 100 Ma.

In addition, climatic effects have to be taken into consideration. Plant material from DSDP site 361 suggests a temperate climate and well-vegetated onshore environment off the Cape Basin (although this is questioned by McLachlan & Pieterse (1978), who suggest a harsh, probably dry climate), whereas in Angola the climate was probably warm and arid to semi-arid (e.g. Siesser 1978: 970; Natland 1978; Melguen 1978). Apart from differences in water temperature and also probably salinity and density, these climatic differences are clearly reflected by the different dominant sedimentary facies in the two basins—that of the Cape Basin being predominantly terrigenous (reflecting active erosion and transport by river systems), whereas that of the Angola Basin is more calcareous and pelagic, in accordance with arid climate and low sediment supply. This in turn may be related to differential nutritional resources in the basins.

To summarize, it would seem simplistic to seek a single cause for the lack of Labeceratinae in the eastern South Atlantic. Prevailing surface currents may have been adequate to assist migration of the Labeceratinae into the Atlantic, but a combination of factors, including physical and chemical differences in the Argentine–Cape and the Brazil–Angola Basins, separated by the aseismic Rio Grande Rise and Walvis Ridge, may have acted selectively in producing this palaeobiogeographical distribution pattern. To these must be added the prime, albeit virtually unknown, factors of differential ecological requirements of the different ammonite taxa, which probably completely overshadow all the other restricting factors.

DESCRIPTION OF A NEW SPECIES

Myloceras bituberculatum sp. nov.

Figs 17–18

Type

Holotype is SAM-PCZ7299a (ex Van Hoepen Collection, uncatalogued specimen); probably from the lower reaches of the Mzinene River, Zululand, Mzinene Formation, Upper Albian.

Material

Paratypes are SAM-PCZ7299b, PCZ7300–7304, PCZ8331–8338 (ex Van Hoepen Collection, uncatalogued specimens); probably all from the lower reaches of the Mzinene River, Zululand, Mzinene Formation, Upper Albian.

Description

The material consists of crioceratitid phragmocones only; the uncoiled section is unknown. Coiling is relatively tight for *Myloceras*, with successive whorls just touching, and the ventral ribs and tubercles of the preceding whorls slightly impressed in the dorsum of succeeding whorls. Umbilical width increases



Fig. 17. *Myloceras bituberculatum* sp. nov. A-C. SAM-PCZ7301. D-E. SAM-PCZ8331. D. $\times 2$, E. $\times 1$. F-G. SAM-PCZ8332. F. $\times 2$, G. $\times 1$. H. SAM-PCZ7299a, holotype. $\times 1$. I-J. SAM-PCZ8333. I. $\times 2$, J. $\times 1$.

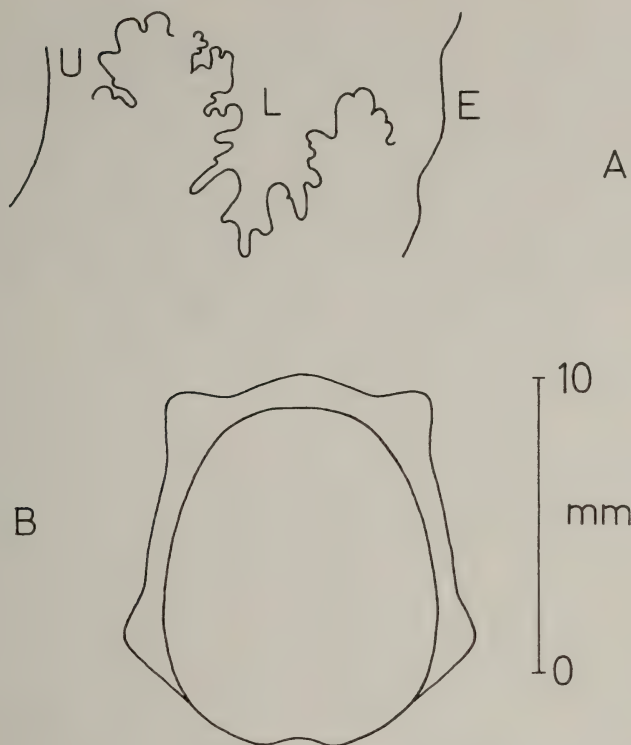


Fig. 18. *Myloceras bituberculatum* sp. nov. A. Suture line of SAM-PCZ7301. B. Whorl section of SAM-PCZ7301. Scale bar to size for A and B.

slightly with growth, in the available material ranging from 36 to 41 per cent of the diameter.

The whorl section is trapezoidal, higher than wide to very compressed, with a narrower venter than dorsum. The flanks are virtually flat (Fig. 18B).

Ornament is very robust, consisting of prominent umbilical tubercles, bifurcating and intercalated ribbing and ventral tubercles. The umbilical tubercles are situated on the outer edge of the umbilical wall, and are conical to radially elongated. From these a prorsiradiate, slightly sinusoidal pair of ribs generally arises. In addition, intercalatory ribs may arise at the umbilical edge or up to a midflank position. On the early whorls of some specimens single ribs, arising at the umbilical tubercles, alternate with intercalatory ribs arising at midflank.

Ventral tuberculation is variable, both within the same or between different specimens. All ribs may bear a pair of distinctly clavate tubercles or major ribs, with prominent clavate tubercles, may alternate with weaker ribs, either without tuberculation at all, or only with weak, conical ventral tubercles. All ribs cross the venter with a slight forward curvature and broadening.

The suture line is only partially exposed in PCZ7301 (Fig. 18A).

Dimensions

<i>Specimen number</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>
PCZ7299a	62	19 (30,6)	21 (33,8)	0,90	24 (33,8)
PCZ7299b	61	16 (26,2)	21 (34,4)	0,76	25 (41)
PCZ7300	—	18 (1)	23 (—)	0,78	—
PCZ7301	51	15 (29,4)	18 (35,3)	0,83	21 (41,2)
PCZ7302	36	10 (27,8)	15 (41,7)	0,67	13 (36,1)
PCZ7303	—	12 (—)	16 (—)	0,75	—
PCZ7304	24	7 (29,2)	9 (37,5)	0,78	9 (37,5)
PCZ8332	26	6 (23,0)	10 (38,5)	0,60	10 (38,5)
PCZ8333	21	5,5 (20,2)	8 (38,1)	0,69	8,5 (40,5)

Discussion

This species and *M. paradoxus* (Collignon, 1964) (see Kennedy 1985: 307–309, figs 11–12) are unique amongst *Myloceras* in possessing distinct umbilical tubercles. *Myloceras bituberculatum* differs from *M. paradoxus* in having much stronger and wider-spaced ribbing. As far as whorl section and frequency of ribbing on the venter are concerned, affinities may be sought with *M. besairiei* Collignon and *M. robustum* Klinger, but the presence of umbilical tubercles clearly distinguishes the present material.

Förster (1975: 185) described part of a crozier with incipient umbilical tubercles from Mozambique as *M. cornucopium*. This fragment has a whorl-section that is wider than high, and I doubt if it can be referred to the present species.

Due to the imprecise locality data I do not know what—if at all, the accompanying *Labeceras* dimorph is.

Occurrence

Upper Albian of Zululand.

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however, I take responsibility for the opinions expressed. Technical assistance by Mss S. Dove, J. Blaeske, and M. Joubert (S.A. Museum) is also gratefully acknowledged. Thanks are due to Mrs S. Saven for typing several drafts of the manuscript.

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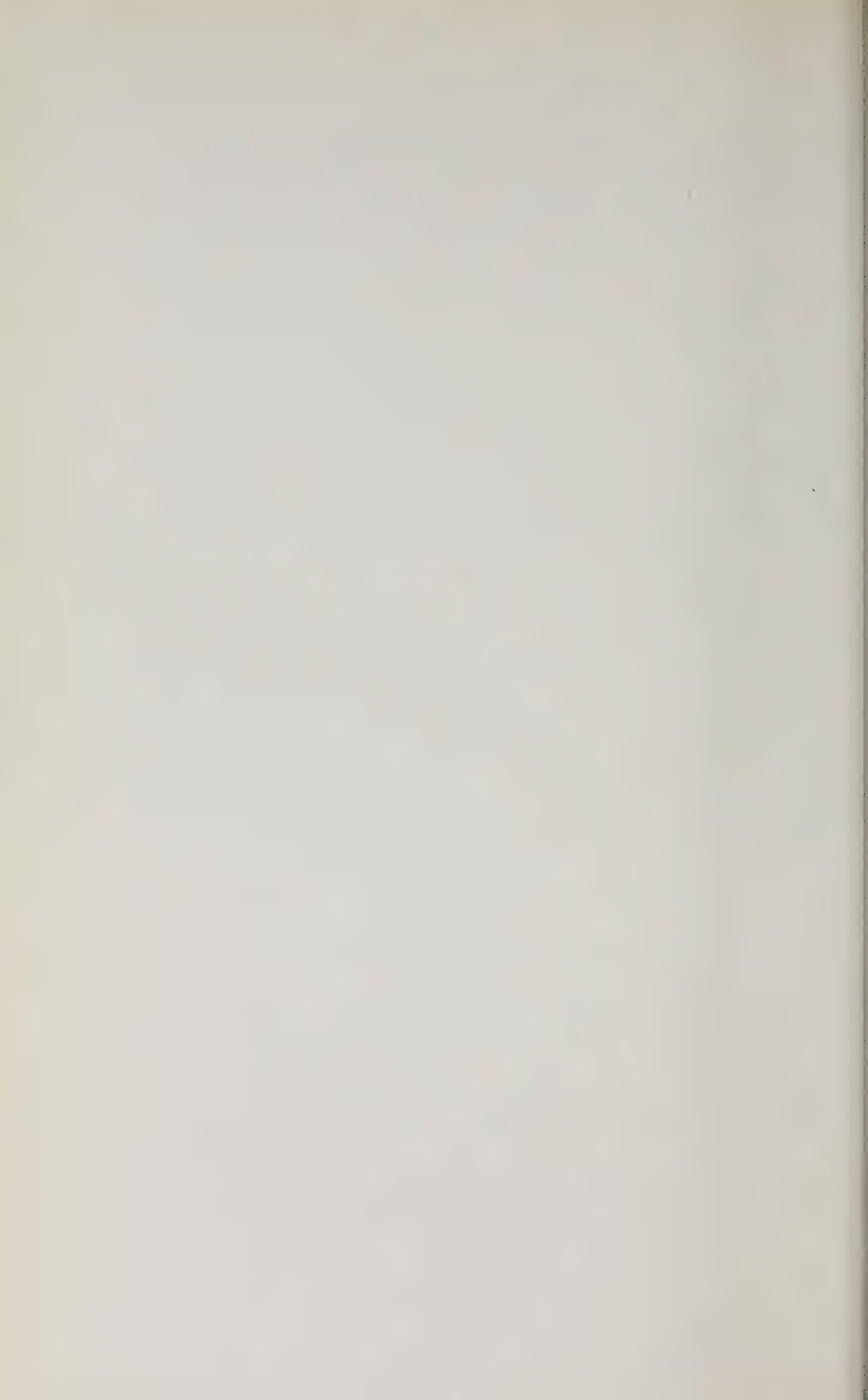
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* Note added at proof stage (see p. 204).

New material has been described from Patagonia (Aguirre Urreta, M. B. & Riccardi, A. C. 1988. Albian heteromorph ammonoids from southern Patagonia, Argentina. *Journal of Paleontology* **62** (4): 598–164). This includes *Labeceras crassetuberculatum* Klinger *magnum* ssp. nov., *L. singulare* (Leanza, 1970) and *Myloceras* (*Calliscaphites*) *andinus* Leanza. *Calliscaphites* is retained as a subgenus of *Myloceras* on account of its alleged crioceratitid coiling. Judging by the compressed whorl section and regular ornament of the type and only species, *M. (C.) andinus*, it appears to be close to the group of *M. besairiei* and '*Ellipsoceras*' *expansum*. On the whole, description of this fauna does not change any of the opinions expressed in this article.



6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers.

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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(a) The Figures, Maps and Tables of the paper when referred to in the text

e.g. '... the Figure depicting *C. namacolus* . . .'; '... in *C. namacolus* (Fig. 10) . . .'

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e.g. Therocephalia, but therocephalian

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Department of Marine Biology, South African Museum, Cape Town

(With 10 figures and 3 tables)

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ABSTRACT

Three large fish specimens, taken with a 180-foot bottom trawl in 780–825 m, west of Cape Point, South Africa, are identified as *Gymnoscopelus (Gymnoscopelus) bolini* Andriashev, 1962, despite the fact that they are severely damaged and totally lack body photophores. They represent not only the most northern record of this Subantarctic species, but also the first record of the species in southern African waters. The distribution of Subantarctic lanternfishes in the eastern South Atlantic is discussed. The northern boundary zone for mesopelagic semi-Subantarctic and bathypelagic Subantarctic species at about 18°S matches the limits for tropical (holotropical), broadly tropical (thermophilic eurytropical and extended Agulhas), and subtropical (bisubtropical and south subtropical) species. The boundary limit for mesopelagic holosubantarctic species lies farther to the south, at about 30°S, and appears to be associated with the northern limit of relatively fresh Antarctic Intermediate Water in this region. Broadly tropical (thermophobic eurytropical) species also demonstrate a southern distributional limit at this latitude in the eastern South Atlantic.

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INTRODUCTION

Biannual, demersal fish-sampling cruises over the South African west coast shelf region (Orange River to Cape Agulhas) have been undertaken on a routine basis by the Sea Fisheries Research Institute (SFRI), Cape Town, since January 1983 (Payne *et al.* 1987). The lanternfishes (Myctophidae) caught during these cruises have not only provided specimens for taxonomic investigation, but have also yielded data for distributional analyses of species in the family (Hulley 1986a, 1986b). Biological hypotheses for the distribution of the pseudoceanic species, *Lampanyctodes hectoris*, which has accounted for up to 42,4 per cent

(451 000 metric tons) of the total annual South African pelagic catch, have been advanced recently by Hulley & Prosch (1987).

During the January 1987 and July 1987 sampling cruises of R.V. *Africana*, several stations were occupied with a 180-foot bottom trawl at depths greater than the usual 500-m isobath limit. Amongst the material from one of these deeper stations were three large, but very badly skinned, myctophid specimens. Since they were totally devoid of body photophores and since myctophid taxonomy is based mainly on photophore grouping and orientation, the identification of the specimens offered a challenge to an otherwise 'Gestalt' process. The identification, coupled mainly with additional data from the 1986 and 1987 SFRI demersal cruises, calls for comment on the oceanic zonal patterning of mesopelagic fishes in the eastern South Atlantic, and the penetration of Subantarctic and Antarctic faunal elements into the region.

MATERIAL AND METHODS

In addition to the three specimens from the eastern South Atlantic, measurements were taken on 27 specimens of *Gymnoscopelus bolini* (SAM-30694, 30695, 30696, 30697, 30698, 30699, 30700, 30701) and 20 specimens of *Gymnoscopelus* (*Gymnoscopelus*) *braueri* (SAM-30702, 30704, 30705, 30706, 30707) from FRV *Walther Herwig* stations in the western South Atlantic. Meristics for specimens of the two species from the same region were extracted from laboratory work-sheets. Distributional records for *G. bolini* have been taken from both published and unpublished sources.

When possible, all counts and measurements were made on the left side. Gill-raker counts (GR) for the first arch do not include stubs. The ultimate ray of both the dorsal and anal fin is double, but has been counted as a single element. Measurements, which were taken to the nearest 0.1 mm with needle-point sliding calipers, included: standard length (SL); head length (HL)—tip of snout to extreme posterior margin of operculum; length of upper jaw (JL)—anterior tip of premaxilla to its posterior end; diameter of eye (ED)—horizontal distance between opposite margins of the socket; depth of head (HD)—vertical through the posterior end of the premaxilla; depth of body (BD)—vertical through the upper base of the pectoral fin; depth of caudal peduncle (CPD)—least vertical depth; predorsal length (PreD)—distance between tip of snout and vertical through base of first dorsal ray; prepectoral length (PreP)—distance between tip of snout and vertical through upper base of pectoral fin; preventral length (PreV)—distance between tip of snout and vertical through base of outermost ray of ventral fin; preanal length (PreA)—distance between tip of snout and vertical through base of first anal ray; pre-adipose length (PreAd)—distance between tip of snout and vertical through origin of adipose fin; and length of caudal peduncle (CPL)—distance between vertical through base of last anal fin ray and end of lateral line.

Photophore groupings and terminology are in accordance with Paxton (1972).

DESCRIPTION OF MATERIAL

Gymnoscopelus (Gymnoscopelus) bolini Andriashev, 1962

Figs 1–10

Lampanyctus nicholsi: Norman, 1930: 326 (*partim*).*Gymnoscopelus (Gymnoscopelus) bolini* Andriashev, 1962: 272, fig. 34 (holotype ZIANL 36383; 53°01'S 109°30'W). Parin *et al.*, 1973: 118, fig. 20; 1974: 109, fig. 11. Krefft, 1974: 232. Wisner, 1976: 210, fig. 197. Post, 1979: 19. Hulley, 1981: 250, fig. 120; 1986c: 299, fig. 86.51. McGinnis, 1982: 61, fig. 50. Bekker, 1983: 220, fig. 90; 1985: 161. Bekker & Evseenko, 1987: 16.*Material*

Three immature female specimens, SAM-31035 (SL 197,7 mm; 220,7 mm; 249,8 mm) trawled west of Cape Point, South Africa; R.V. *Africana* (SFRI station A5280 050 E16; 34°21,8'S 17°38,4'E; 18 January 1987; 19h30–20h30 (local); BT-180'; 780–825 m; bottom temperature not measured).

Description

Measurements expressed as a percentage of SL are given in Table 1.

D 21–22; A 20–22; P 12–13; V 8; GR 6 + 1 + 15, total 22; AO and Prc photophores missing.

TABLE 1

Measurements expressed as a percentage of the standard length (SL) for *Gymnoscopelus (Gymnoscopelus) bolini* (SAM-31035) from the eastern South Atlantic.

SL	197,7 mm	220,7 mm	249,8 mm
HL	25,9	24,3	25,3
JL	19,8	19,1	19,7
ED	5,2	5,6	5,1
HD	18,4	17,2	17,1
BD	17,5	18,7	19,1
CPD	10,1	9,6	—
CPL	20,1	18,6	20,6
PreD	36,2	39,3	38,8
PreP	24,4	25,5	25,8
PreV	40,2	43,8	40,9
PreA	57,3	59,4	58,6
PreAd	78,4	79,1	70,4

Body fusiform and somewhat laterally compressed, length of head 3,9–4,1 in SL. Mouth terminal, slightly oblique and extending well behind vertical through posterior margin of orbit; length of upper jaw 5,1–5,2 in SL and 1,3 in head length; anterior dentigerous region of premaxilla not expanded; maxilla only slightly expanded posteriorly. Teeth on premaxilla and dentary small and conical, none enlarged; palatines with series of minute teeth along anterior two-

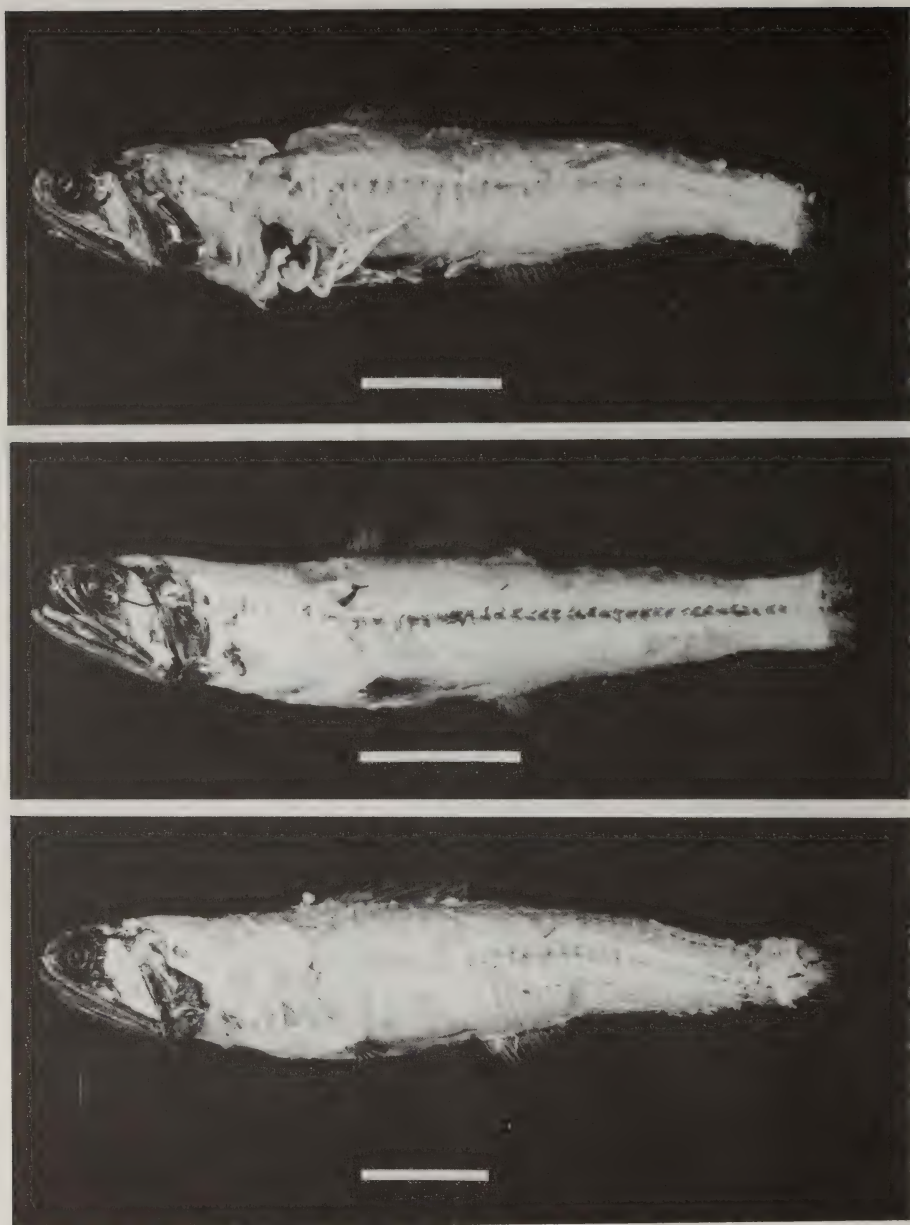


Fig. 1. *Gymnoscopelus (Gymnoscopelus) bolini* (SAM-31035). Lateral view of specimens. SL 220,7 mm; SL 197,7 mm; 249,8 mm (top to bottom). Scale = 40 mm.



Fig. 2. *Gymnoscopelus (Gymnoscopelus) bolini* (SAM-31035). Lateral view of head.
SL 220,7 mm. Scale = 10 mm.

thirds, some teeth at antero-dorsal margin enlarged and hooked; mesopterygoids with small teeth. Eye large, its diameter 4,3–5,1 in length of head, situated normally so that vertical distance between upper lip and lower margin of eye at middle of orbit, about equal in length to pectoral base. Postero-dorsal margin of operculum evenly concave. Origin of dorsal fin in front of vertical through outer base of ventral fin. Pectorals damaged, but probably short and reaching only about one-half to two-thirds the distance to ventral origin. Ventrals reaching to anus. Anal origin under posterior third of base of dorsal fin; length of base of anal fin about equal to dorsal base. Origin of adipose fin on or only slightly in advance of vertical through base of last anal ray. Length of caudal peduncle about equal to or only slightly longer than length of upper jaw. Seven dorsal and 9–10 ventral procurent caudal rays, well developed, spine-like and posteriorly curved.

Antorbital luminous tissue well developed at antero-ventral margin of orbit, extending dorsally between nasal capsule and eye to about level of dorsal margin of capsule, and surrounded by black-pigmented skin. Three Br photophores on each side, under lower jaw. Op_1 small, opposite posterior end of upper jaw; Op_2 large, above and behind Op_1 at overlap of dorsal and ventral preopercular flanges. Body photophores missing, specimens very badly skinned.

Colour. Flesh pale, but head with torn patches of dark-brown skin; iris chocolate-brown; fin rays pigmented; mouth and gill cavities dark.

DISCUSSION

The body form and fin ray distributions, the presence of an adipose dorsal fin, three Br photophores under the lower jaw, and Op₁ and Op₂ photophores confirm the family identity of the specimens. Further, the length of the upper jaw and the structure of the dorsal and ventral procurent rays suggest inclusion within the subfamily Lampanyctinae. Within the subfamily, only the genera *Notoscopelus*, *Scopelopsis* and *Gymnoscopelus* (*Gymnoscopelus*) have 21 or more dorsal fin rays, and only *Notoscopelus* and *Gymnoscopelus* (*Gymnoscopelus*) have 20 or more anal fin rays (Paxton 1972, table 8; Hulley 1981). In both *Notoscopelus* and *Scopelopsis* the origin of the anal fin is on a vertical through the middle of the dorsal fin base, whereas in *Gymnoscopelus* the origin is on a vertical through the posterior third of the dorsal fin base. This feature is evident even in larval forms of these genera (Moser & Ahlstrom 1972, figs. 12A, D; 1974, fig. 12; Moser *et al.* 1984, figs 120F, 121B, D). Further, whereas the Op₁ is normally positioned in *Scopelopsis*, the Op₂ is absent from its position under the overlap region between the dorsal and ventral preopercular flanges. It may be represented by a photophore that is reduced in size to that of a 'secondary' photophore and is positioned postero-ventrally to the overlap region (SAM-28664—4 specimens; SAM-28657—1 specimen). The diagnostic character given by Paxton (1972), namely the anterior part of premaxillary with (*Notoscopelus*) or without (*Gymnoscopelus*) expanded dentigerous area, is open to question. Examination of specimens of *Notoscopelus* has revealed that the dentigerous area is expanded in *N. (Notoscopelus) caudispinosus* (SAM-29245—8 specimens), somewhat expanded in *N. (Notoscopelus) kroeyerii* (SAM-29529—5 specimens) and *N. (Pareiophus) bolini* (SAM-29497—2 specimens), and without an anterior expansion in *N. (Notoscopelus) resplendens* (SAM-30824—4 specimens). Finally, the size of the three large specimens (198–250 mm) precludes their identification in either *Scopelopsis* or *Notoscopelus*; *S. multipunctatus* attains a maximum length of 81 mm, *N. caudispinosus* a length of 140 mm, *N. kroeyerii* 143 mm, *N. resplendens* 95 mm, and *N. bolini* 102 mm, in the Atlantic Ocean (Hulley 1981).

The genus *Gymnoscopelus* comprises two subgenera, differentiated by the position of PVO₂ below (subgenus *Gymnoscopelus*—4 species) or above (subgenus *Nasolychnus*—4 species) the level of the upper base of the pectoral fin. Unfortunately, this photophore is missing in the three specimens (SAM-31035). However, only two species in the genus match the specimens in gill-raker count, namely *G. (G.) bolini* with GR 6 (rarely 7) + 1 + 15 (14–16, rarely 13); and *G. (G.) braueri* with GR 6 (7) + 1 + 15–16 (17, rarely 14 or 18). Distributions for these counts are given in Table 2. GR₁ and anal fin ray counts partially overlap in these two species and are therefore not entirely suitable as diagnostics for the separation of these two species. However, the position of the origin of the dorsal fin in relation to the origin of the ventral fin is diagnostic. In *G. bolini* the dorsal origin is anterior to the vertical through the outer base of the ventral

TABLE 2

Dorsal, anal and gill-raker counts for *Gymnoscopelus (Gymnoscopelus) bolini* and *Gymnoscopelus (Gymnoscopelus) braueri* from the western South Atlantic, and *Gymnoscopelus (Gymnoscopelus) bolini* (SAM-31035) from the eastern South Atlantic.

Count		Number of specimens											
		6	7	13	14	15	16	17	18	19	20	21	22
Dorsal	<i>G. bolini</i>									8	11	24	8
	SAM-31035										1	2	
	<i>G. braueri</i>				2	28	109	25					
Anal	<i>G. bolini</i>									1	9	40	12
	SAM-31035										1	1	1
	<i>G. braueri</i>						1	47	107	8	1		
GR _u	<i>G. bolini</i>	74	4										
	SAM-31035	3											
	<i>G. braueri</i>	211	31										
GR _l	<i>G. bolini</i>			3	14	53	6						
	SAM-31035				3								
	<i>G. braueri</i>				3	118	112	8	1				

fin, whereas in *G. braueri* the origin is posterior to the vertical through the outer base of the ventral fin. This is evident from the differences in the slopes of the regressions of PreD against SL (Fig. 3) and of PreD against PreV (Fig. 4), since the ventral fin is similarly positioned in the two species (Fig. 5). In addition, the length of the caudal peduncle (CPL) in *G. bolini* is shorter than its length in *G. braueri* (Fig. 6). Values of the meristics and morphometrics for the three R.V. *Africana* specimens therefore confirm their identity as *G. bolini*. This conclusion is supported by the large size of the specimens—*G. bolini* attains a maximum length of 280 mm, whereas *G. braueri* attains only a maximum length of 132 mm—and by comparison of scatter-plots of their morphometrics with those of other specimens of *G. bolini* (Figs 7–9).

The distribution of *Gymnoscopelus (Gymnoscopelus) bolini* is given in Figure 10.

The species has been trawled pelagically between the Antarctic Polar Front (APF) and the Subtropical Convergence (STC), and a Subantarctic distribution pattern (Parin *et al.* 1974; Hulley 1981, in press) or west wind drift distribution pattern (Krefft 1974) has been proposed. Size diminution with decreasing latitude observed by McGinnis (1982) was not evident in the western South Atlantic (Hulley 1981), where large specimens (greater than 130 mm) have been taken as far north as the STC, but at depths greater than 600 m. Hulley (1981) therefore proposed that the distribution of *G. bolini* could be correlated with the spread of Antarctic Intermediate Water. He suggested temperature limits between 1,0°C–2,0°C and 5,0°C–5,5°C for adults, and pointed out that juveniles were taken in water temperatures of 12°C–13°C.

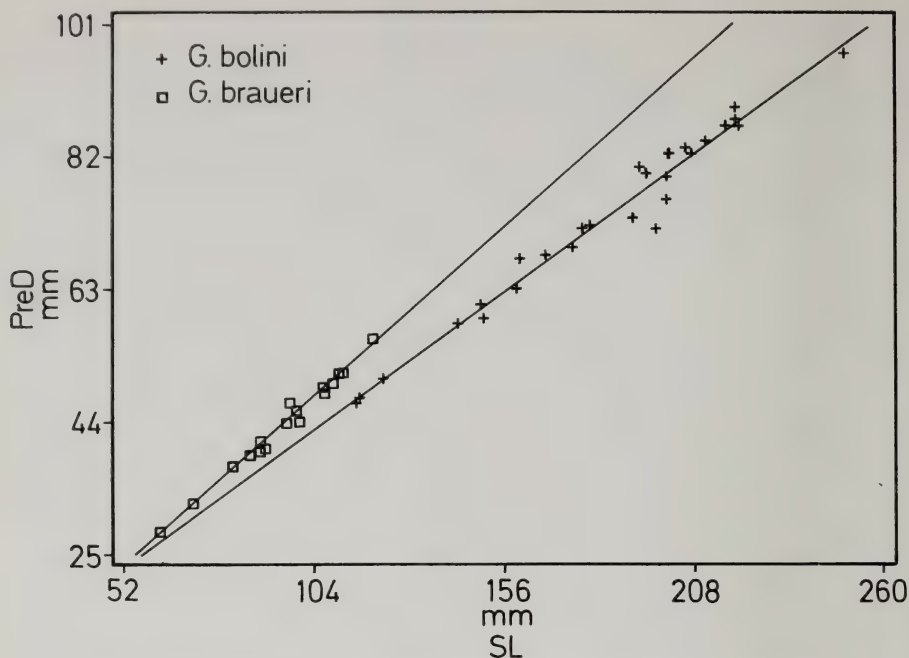


Fig. 3. Regression of predorsal length (PreD) against standard length (SL) for *Gymnoscopelus* (*G.*) *bolini* (+) and *Gymnoscopelus* (*G.*) *braueri* (□).

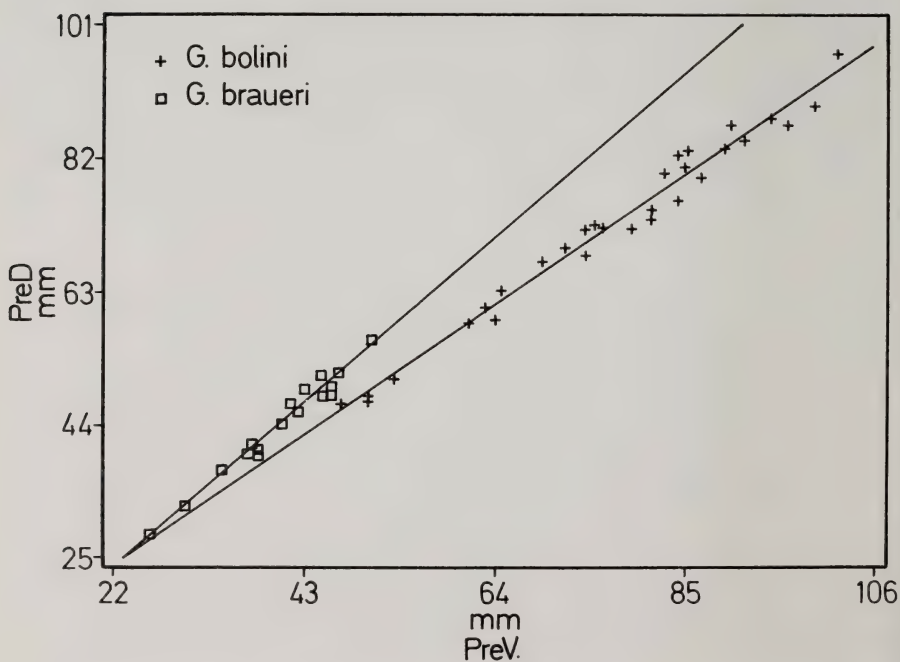


Fig. 4. Regression of predorsal length (PreD) against preventral length (PreV) for *Gymnoscopelus* (*G.*) *bolini* (+) and *Gymnoscopelus* (*G.*) *braueri* (□).

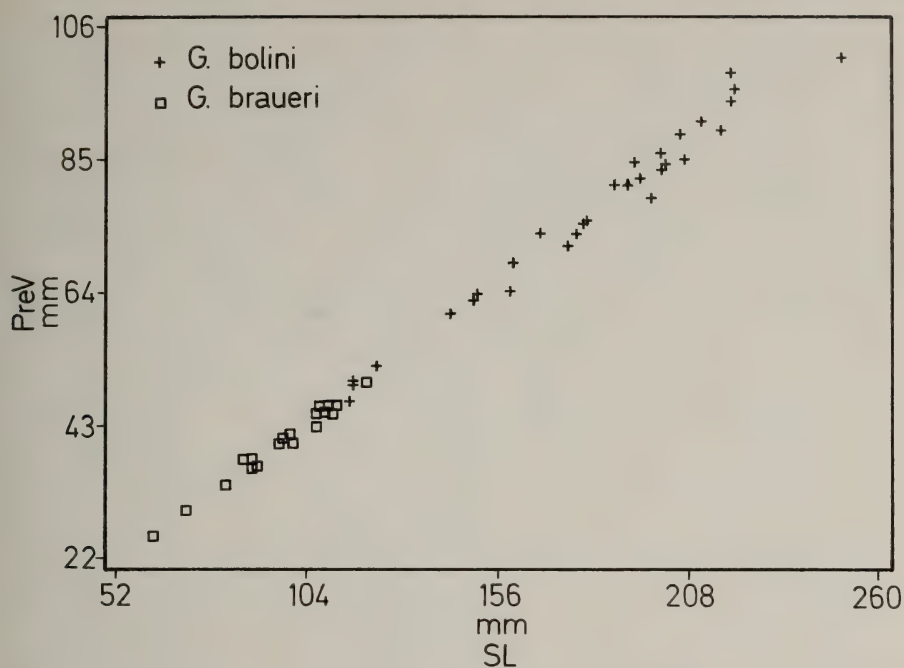


Fig. 5. Scatter-plot of preventral length (PreV) against standard length (SL) for *Gymnoscopelus* (*G.*) *bolini* (+) and *Gymnoscopelus* (*G.*) *braueri* (□).

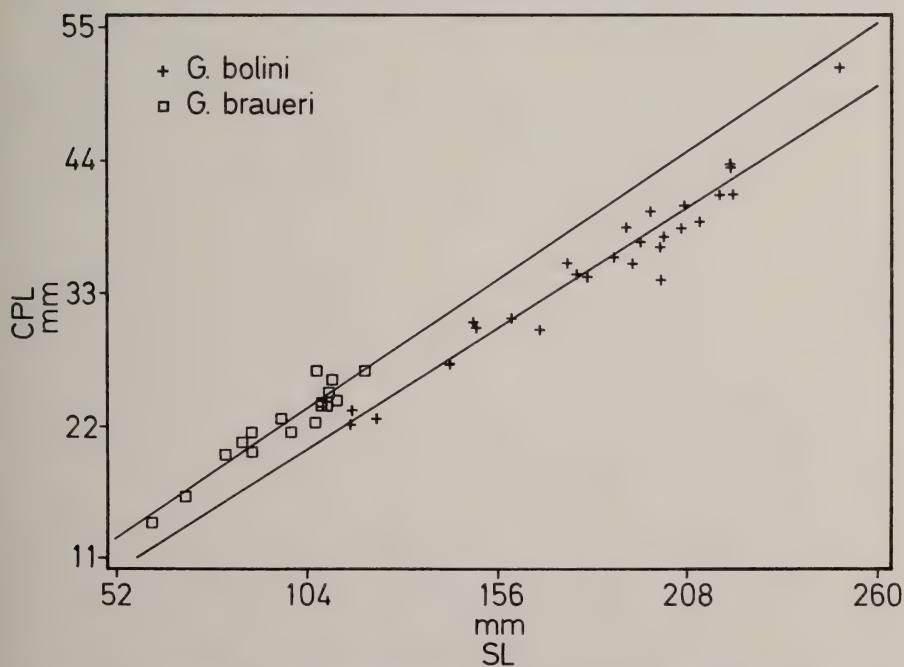


Fig. 6. Regression of caudal peduncle length (CPL) against standard length (SL) for *Gymnoscopelus* (*G.*) *bolini* (+) and *Gymnoscopelus* (*G.*) *braueri* (□).

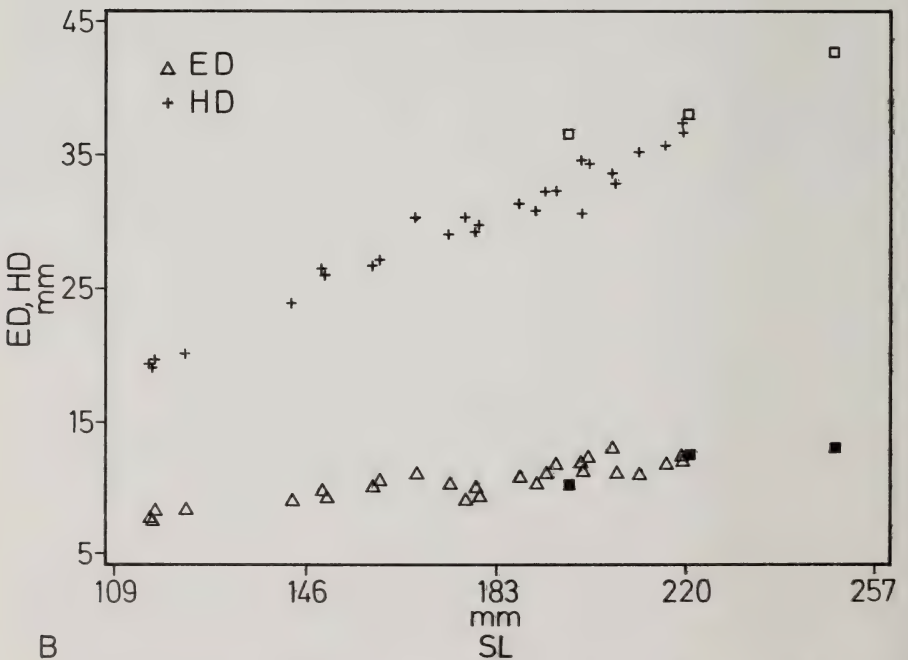
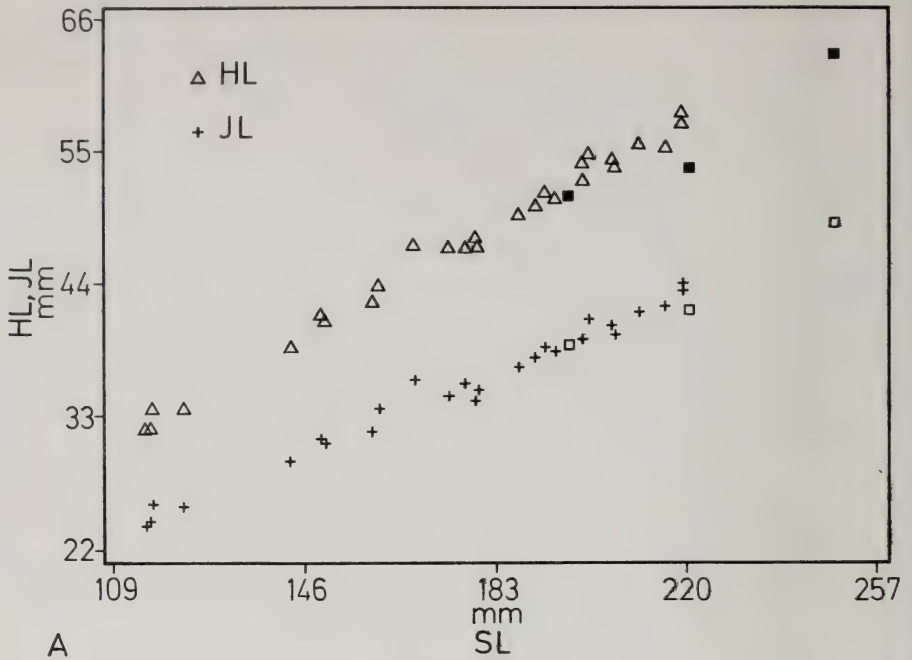
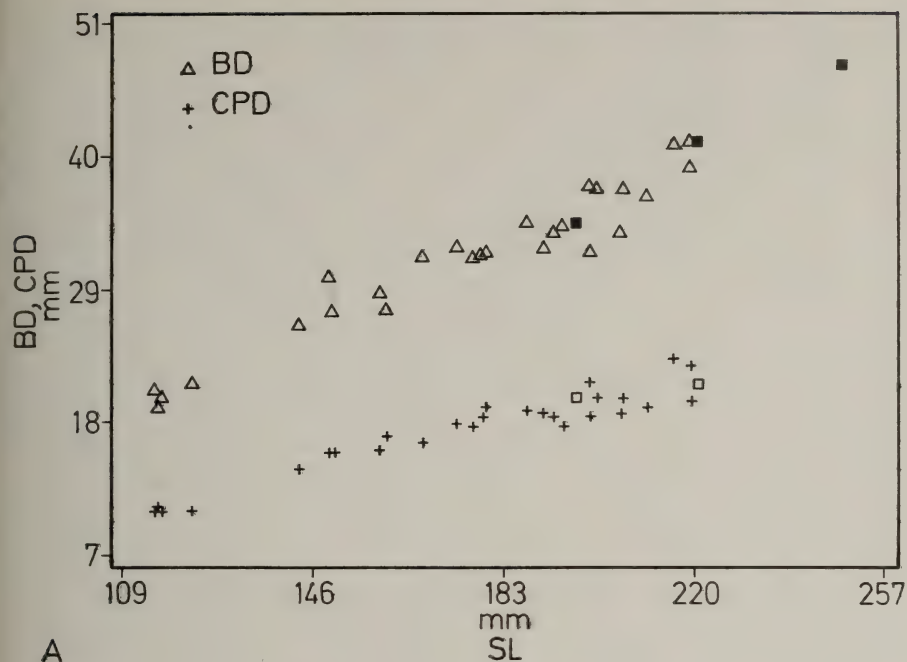
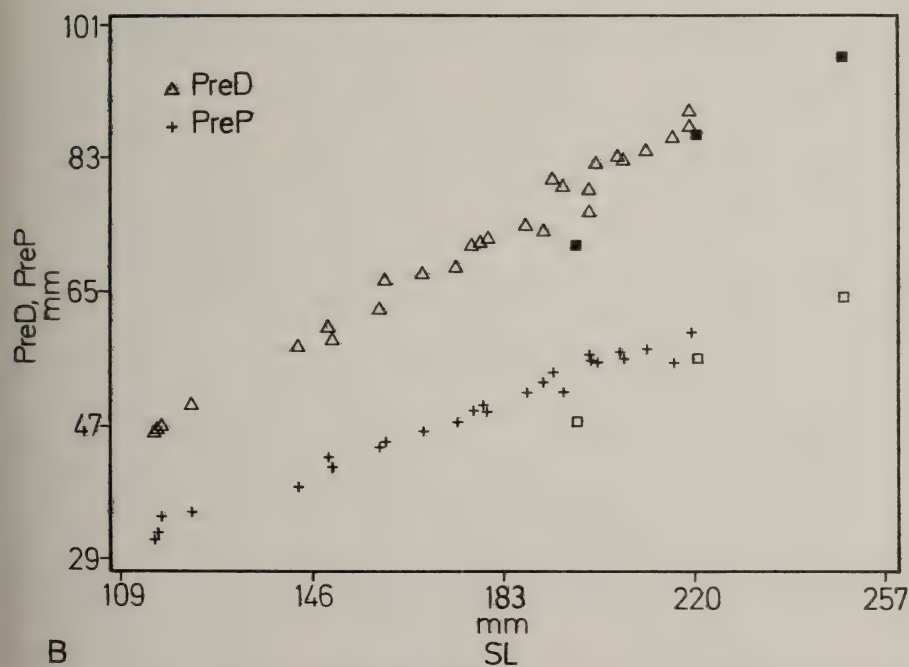


Fig. 7. Scatter-plots of *Gymnoscopelus (G.) bolini*. A. Head length (HL) and length of upper jaw (JL) against standard length (SL). B. Eye diameter (ED) and head depth (HD) against standard length (SL). Open and solid square symbols refer to SAM-31035 specimens.



A



B

Fig. 8. Scatter-plots of *Gymnoscopelus (G.) bolini*. A. Body depth (BD) and caudal peduncle depth (CPD) against standard length (SL). B. Predorsal length (PreD) and prepectoral length (PreP) against standard length (SL). Open and solid square symbols refer to SAM-31035 specimens.

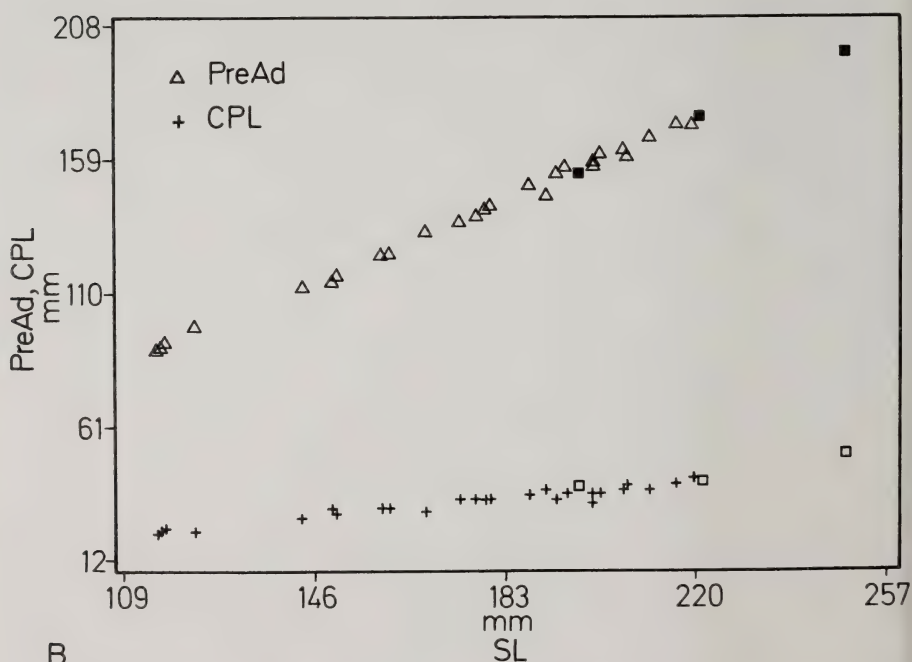
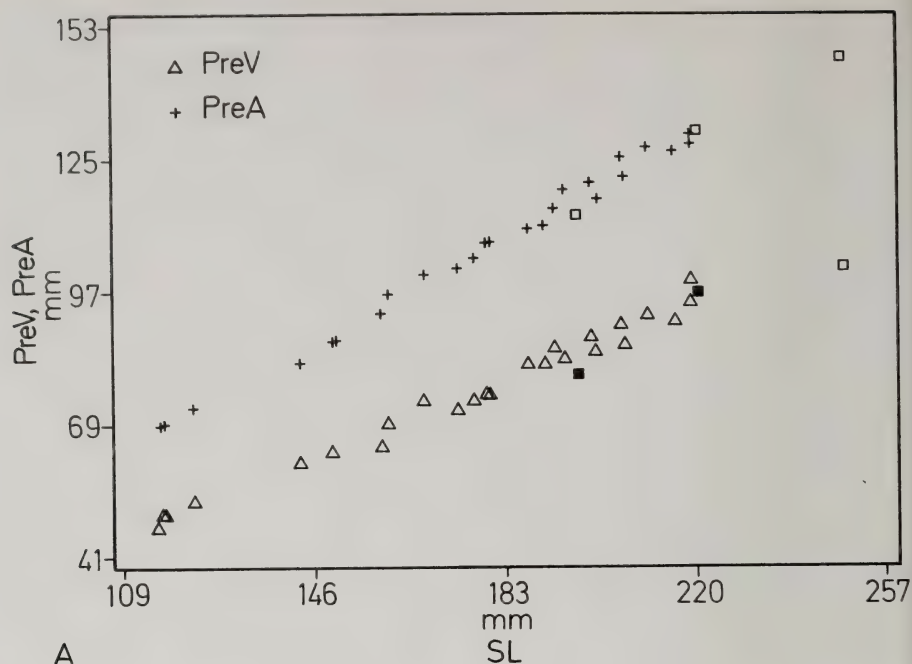


Fig. 9. Scatter-plots of *Gymnoscopelus* (*G.*) *bolini*. A. Preventral length (PreV) and preanal length (PreA) against standard length (SL). B. Pre-adipose length (PreAd) and caudal peduncle length (CPL) against standard length (SL). Open and solid square symbols refer to SAM-31035 specimens.

An adult epibenthic distribution, with probable spawning at depth, has been suggested by Hulley (1981, in press). In the Atlantic, large specimens of *G. bolini* (usually greater than 200 mm) have been reported from benthic sampling along the Argentinian slope north to about 38°S (Hulley 1981). More recent unpublished data (ISH) extend this benthic range northwards (WH 703/78: 35°49,2'S 52°49,7'W; 750 m; T_b 4,2°C) to approximate more closely the southern limit of the STC and the position of the pelagic biogeographic boundary in this region (Boltovskoy 1970, 1986). The species has also been taken with a beam trawl in the southern Indian Ocean (48°43,5'S 71°06,5'E; 937 m) (Hulley *et al.* in press).

Therefore, the three R.V. *Africana* specimens not only represent the most northerly record for this Subantarctic species and the first record in southern African waters, but they also mirror the benthic distribution of *G. bolini* on the South American slope.

The effect of meridional current flow skews the zonal patterns of the distributions of oceanic fishes, particularly those of mesopelagic species (*vide* Hulley 1981, fig. 30). Drift-card observations have confirmed the northward flow of surface water from the STC towards the South African coast in winter (Shannon *et al.* 1973), while subsurface investigations have revealed a complex cold-core eddy system to depths of 500 m and more, north of the STC to about 31°S (Visser 1969; Shannon & Van Rijswijk 1969; Welsh & Visser 1970; Henry 1975; Lenz 1975; Allanson *et al.* 1981; Lutjeharms 1981; Lutjeharms & Emery 1983; Lutjeharms *et al.* 1985). Recently, Gordon *et al.* (1987: 586) described how South Atlantic Water, a blend of thermocline water and Subantarctic Surface Water (identical in temperature and salinity to South Atlantic varieties of Antarctic Intermediate Water—McCartney 1977), may be 'swept into the Retroflexion region to the east of each of the Agulhas rings'. Pulsed intrusions of cold Subantarctic Surface Water have been observed crossing the STC into the southern Benguela Region as an inherent part of the spawning and separation of an Agulhas ring (Lutjeharms & Meeuwis 1987; Lutjeharms & Van Ballegooyen in press, fig. 9). Isotherm and isohaline distributions given by Gorshkov (1978) suggest that this 'cold corridor', linking the offshore Benguela System with the Subantarctic, is a regular feature of the region. Biologically, this feature is well exemplified by the distribution of the Subantarctic copepod *Metridia lucens* (De Decker 1984, figure on p. 355), where the longitudinal axis of the penetration of this species into the southern Benguela Region matches the average longitude (18°25'E) of the cold wedge feature (Lutjeharms & Van Ballegooyen in press).

The occurrence of Antarctic and Subantarctic midwater fishes in the eastern South Atlantic is therefore to be expected and is confirmed by myctophids and other species, e.g. *Benthallbella macropinna* (Scopelarchidae), *Bathylagus antarcticus* (Bathylagidae), *Melanostigma gelatinosum* (Zoarcidae), *Scopelosaurus hamiltoni* (Notosudidae), *Borostomias antarcticus* (Astronesthidae), *Melanonus gracilis* (Melanonidae), *Woodsia meyerwaardeni* (Photichthyidae), *Cerati*

tentaculatus (Ceratiidae), *Paradiplospinus gracilis* (Gempylidae) and *Sio norden-skjoeldi* (Melamphaidae) (Hulley 1972; Johnson 1974; Bertelsen *et al.* 1976; Krefft 1978; Anderson 1986; Cohen 1986; Gibbs 1986).

For the Myctophidae, Hulley (1986b) has pointed out that holosubantarctic and semi-Subantarctic species make up about 16 per cent by number of the oceanic, mesopelagic myctophid fauna in the southern Benguela Region. Although certain Subantarctic Pattern species (*Protomyctophum choriodon*, *P. gemmatum*, *Electrona subaspera*, *Gymnoscopelus fraseri*, *G. hintonoides*, *G. microlampas*), Broadly Antarctic Pattern species (*Krefftichthys anderssoni*, *Protomyctophum bolini*, *P. tenisoni*, *Gymnoscopelus braueri*, *G. nicholsi*) and Antarctic Pattern species (*Electrona antarctica*) have not yet been recorded, an analysis of nine species representing these pattern types that do occur in the eastern South Atlantic is presented in Table 3. However, the following should be noted: firstly, a single specimen of *Lampanyctus achirus* was recorded from 21°05'S 02°00'W (outside the defined region) during Transect-II of FRV *Walther Herwig* (Station WH 443/71); and secondly, Rubiés (1985) recorded *Diaphus hudsoni* from 18°01'S and *Metelectrona ventralis* from 20°50'S off the South West African–Namibian coast.

From Table 3, and with regard to the above, the northern limit of the bathypelagic Subantarctic species, *Lampanyctus achirus*, extends to about 21°S and at depths below 300 m in the eastern Atlantic. With the exception of *Gymnoscopelus piabilis*, this northern limit is matched by mesopelagic semi-Subantarctic species. These species extend to about 18°S and at depths of 10–1 550 m during pelagic sampling and 229–823 m during benthic sampling. On the other hand, mesopelagic holosubantarctic species appear to be limited to the region south of 30°S and at deeper levels, i.e. 300–1 400 m (pelagic sampling) and 780–825 m (benthic sampling). The concept of these two latitudinal boundary zones is reinforced by the observations of Olivar (1987), who pointed out that *Diaphus hudsoni* larvae were most abundant in two particular areas, one around 20°S and the other between 29°S and 30°S, over bottom depths of 400–600 m. Hulley (1981: 284) pointed out that *G. piabilis* represents an 'anomalous case of a semi-subantarctic species', whose distribution is similar to that of a holosubantarctic species. The results expressed in Table 3 confirm this observation. It should be noted that a Holosubantarctic Subpattern for the species has been suggested by both McGinnis (1982)(= Pattern III) and Bekker & Evseenko (1987)(= Notal).

Hulley (1981) has already commented on the distribution of *Lampanyctus achirus* and on the '18°S' boundary zone, the region where the Benguela Current turns to flow westwards (Moroshkin *et al.* 1970). This zone, which may vary seasonally in position and may be farther to the south closer inshore, apparently limits the distribution of broadly tropical species (Thermophilic eurytropical and Extended Agulhas subpatterns), tropical species (Holotropical Subpattern) and subtropical species (Bisubtropical and South subtropical subpatterns). On the other hand, broadly tropical (Thermophobic eurytropical)

TABLE 3

Mesopelagic and bathypelagic Subantarctic species of Myctophidae taken in the eastern South Atlantic (18°–45°S 00°–20°E) during sampling cruises by South African Museum (Cape Town), Sea Fisheries Research Institute (Cape Town), Institut für Seefischerei (Hamburg) (Hulley 1981), and Instituto de Ciencias del Mar (Barcelona) (Macpherson 1986). Bottom depths at all stations greater than 229 m. Distribution pattern nomenclature and limiting temperatures after Hulley (1981).

Species	Limiting/Temp. lower (°C)	upper (°C)	Gear type	No. of stations	No. of specimens	Most northerly position	Fishing depth (m)
BATHYPELAGIC							
Subantarctic							
<i>Lampanyctus achirus</i>		4	pelagic	15	222	27°14'S 05°22'E*	120–1 000
MESOPELAGIC							
Subantarctic (Holosubantarctic)							
<i>Electrona carlsbergi</i>		5	pelagic	1	2	34°26'S 14°43'E	305
<i>Gymnoscopelus bolini</i>	1	5,5	benthic	1	3	34°22'S 17°38'E	780–825
<i>Protomycotophum andriashevi</i>	2	7†	pelagic	1	1	29°30'S 10°03'E	1 400
<i>Protomycotophum parallelum</i>	2	8	pelagic	2	2	38°00'S 15°00'E	600–700
Subantarctic (semi-Subantarctic)							
<i>Diaphus hudsoni</i>	5	15†	pelagic	81	678	18°20'S 10°47'E*	25–600
			benthic	9	12+	26°36'S 13°35'E	425–769
<i>Gymnoscopelus piabilis</i>	3	14	pelagic	3	6	34°12'S 16°35'E	112–1 550
			benthic	1	3	30°10'S 14°50'E	460–495
<i>Metelatrona ventralis</i>	5	15	pelagic	25	96	25°15'S 13°27'E*	10–700
			benthic	2	3	32°15'S 16°25'E	300–425
<i>Symbolophorus boops</i>		15★	pelagic	26	381	19°19'S 14°12'E	10–1 000
			benthic	43	2 647+	23°02'S 13°05'E	229–823

*—see text for further discussion;

★—limiting temperatures at 100 m;

†—limiting temperatures at 200 m.

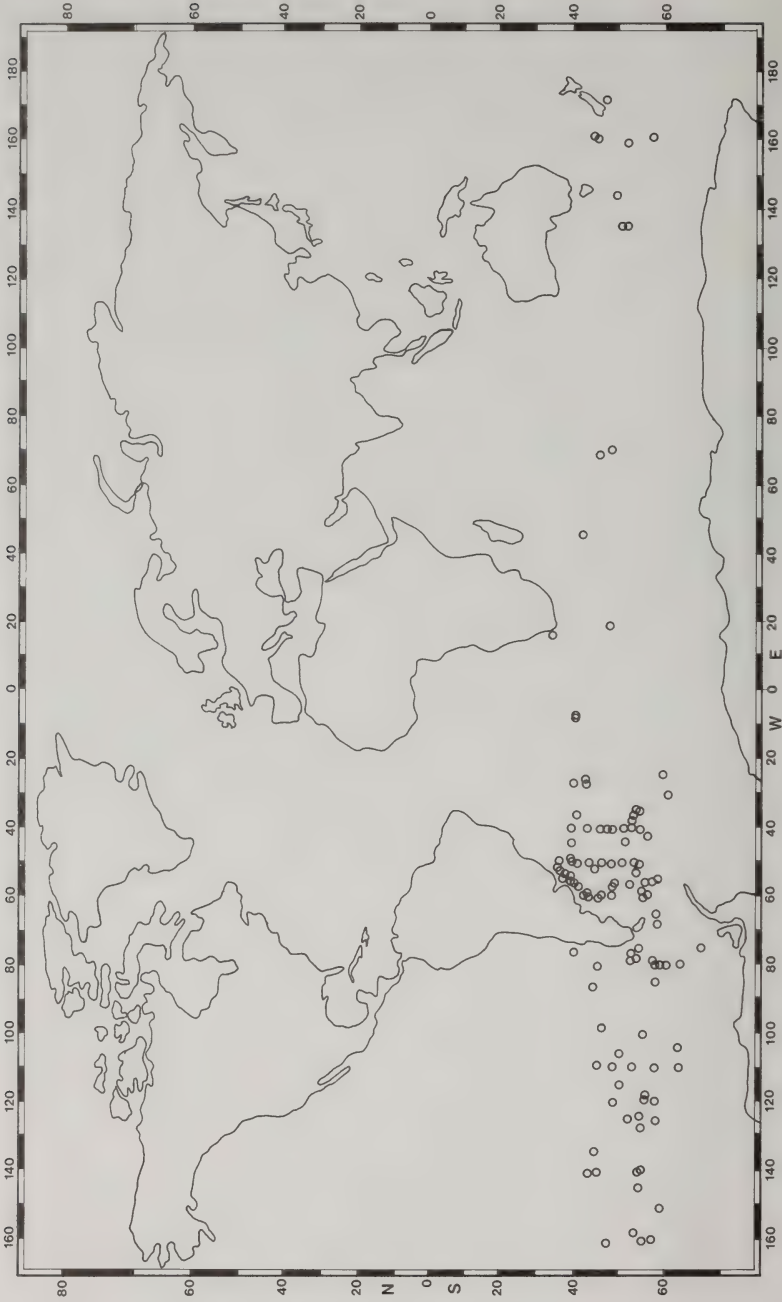


Fig. 10. Distribution of *Gymnoscopelus (Gymnoscopelus) bolini* based on published and unpublished data.

species extend to about 30°S. Despite differences in the distributional limiting temperatures (Table 3), the apparent distributional limit between about 30°S and 38°S is difficult to reconcile with physical hydrographic conditions in the region. However, Shannon & Hunter (in press) recently pointed out that relatively fresh Antarctic Intermediate Water is present off the south-western Cape between Cape Point (34°21'S) and Cape Columbine (32°50'S), and Chapman & Shannon (1985) discussed 'virgin' Central Water upwelling in the region. It is interesting to note that the proposed temperature limits, i.e. 1°C–8°C for holosubantarctic species, and 5°C–15°C for semi-Subantarctic species (excluding *G. piabilis*) (Table 3), approximate temperature values in the T–S curve for Antarctic Intermediate Water (4°–6°C, $<34,7 \times 10^{-3}$) and South Atlantic Central Water (6°C, $34,5 \times 10^{-3}$ to 16°C, $35,5 \times 10^{-3}$), respectively (Shannon 1985; Shannon & Hunter in press). According to the latter authors, statistically significant seasonal differences in the occurrence of Antarctic Intermediate Water were not apparent in the region west of 20°E, although water of lower salinity may be present at 30°–32°S during the summer. Existing data on myctophids preclude elucidation of seasonal trends, since regular sampling was restricted to a few months only. Bathypelagic Subantarctic species were taken in March, April and August; mesopelagic holosubantarctic species in January, March and August; and mesopelagic semi-Subantarctic species in January, February, March, April, May, June, July, August, September and November (SAM data).

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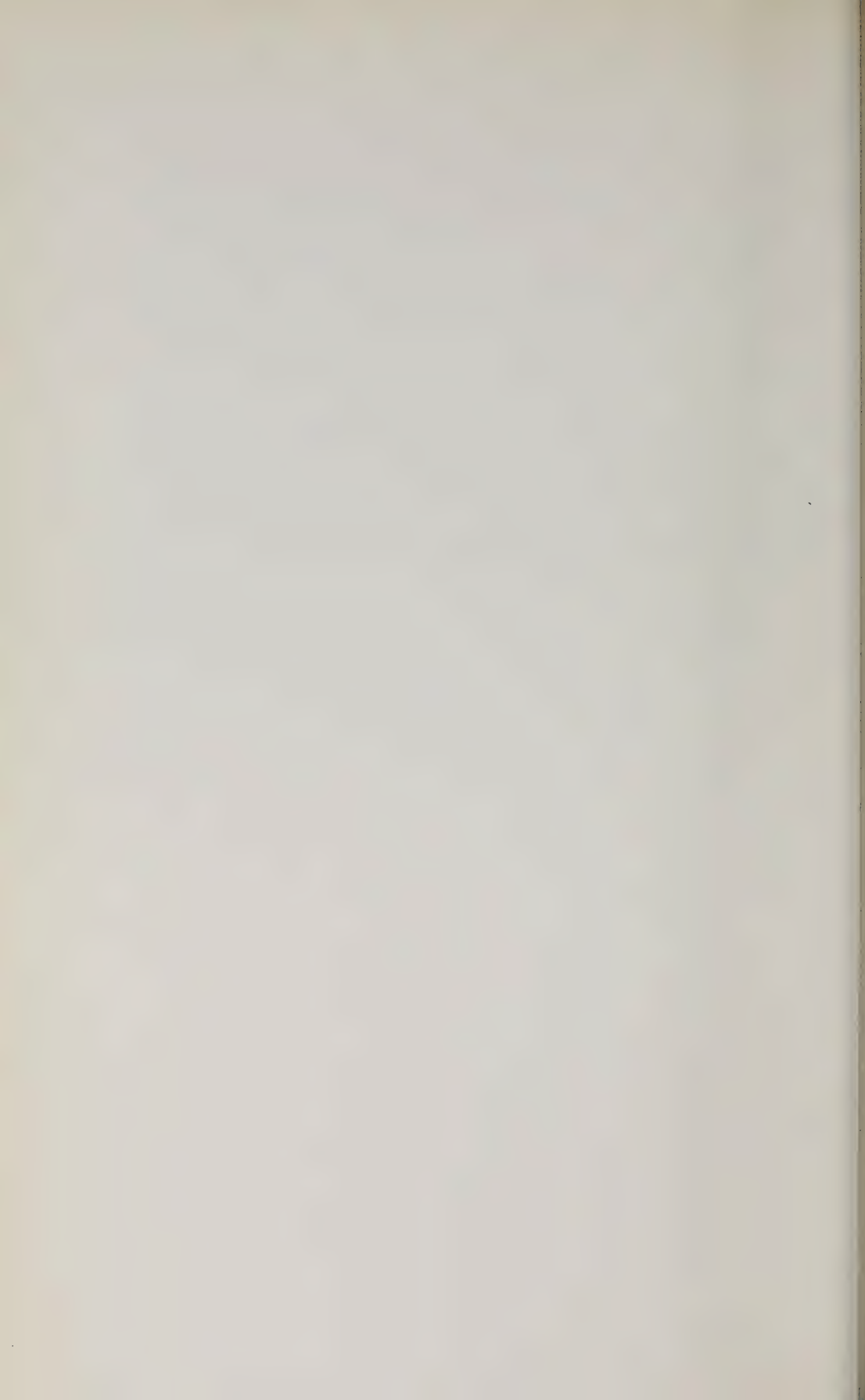
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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

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P. ALEXANDER HULLEY

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WATERS, WITH COMMENTS ON
THE DISTRIBUTION OF SUBANTARCTIC
MYCTOPHIDS IN THE EASTERN
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THE AMMONITE FAMILY
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HYPENGONOCERAS SPATH, 1924

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[MS accepted 27 May 1987]

ABSTRACT

The systematics of the ammonite family Placenticeratidae are complex. Most of the confusion surrounding the plethora of names applied to the family has been cleared by Kennedy & Wright (1983). This confusion was due mainly to failure to recognize intraspecific variation, dimorphism, differing rates of ontogenetic development, slow phylogenetic change, and possibly effects of ecophenotypic variation. The Zululand representatives of this family, *Placenticeras kaffrarium* Etheridge, 1904, from the Middle Coniacian, and *Hoplitoplacenticerus howarthi* Collignon, 1970, in the Upper Campanian, illustrate all these features and permit meaningful discussion. A list of species that have been referred to the family is given. The appendix contains original (or translations of) diagnoses of genera placed in the synonymy of the genus *Placenticerus*. The systematic position of the genus *Hypengonoceras*, which in the past had often been referred to the family Placenticeratidae, is discussed. It is referred to the Engonoceratidae on account of its sutural development.

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INTRODUCTION

In Zululand and Natal, South Africa, the family Placenticeratidae is represented by two species only, *Placenticer* *kaffrarium* Etheridge, 1904, in the Middle Coniacian (*sensu* Klinger & Kennedy 1984), and *Hoplitoplacenticer* *howarthi* Collignon, 1970, in the Upper Campanian. The large population of *P. kaffrarium* permits meaningful discussion on the taxonomy of the family, which should be seen as supplementary to Kennedy & Wright's (1983) pioneering study of *Ammonites polyopsis* Dujardin.

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the repositories of the material studied:

BMNH	British Museum (Natural History), London
EMP	École des Mines Collections, Université Claude-Bernard, Lyons
FSR	Faculté des Sciences, Rennes
MNHP	Muséum National d'Histoire Naturelle, Paris
NMB	National Museum (Bloemfontein) (presently in the collections of the South African Museum, Cape Town)
NMP	Natal Museum, Pietermaritzburg
OUM	Oxford University Museum
SAM	South African Museum, Cape Town
SAS	Geological Survey of South Africa, Pretoria
SP	Collections of the Sorbonne, now in Université Pierre et Marie Curie, Paris

FIELD LOCALITIES

Details of field localities are given by Kennedy & Klinger (1975); fuller descriptions of these localities are deposited in the Department of Palaeontology, British Museum (Natural History), London; Geological Survey of South Africa, Pretoria, and the South African Museum, Cape Town.

DIMENSIONS OF SPECIMENS

All dimensions are given in millimetres: D = diameter; Wb = whorl breadth; WH = whorl height; U = umbilical diameter. Ut, Lt and Vt respectively refer to the number of umbilical, lateral and ventral tubercles. Figures in parentheses are dimensions as a percentage of the total diameter.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916) reviewed and discussed by Kullmann & Wiedmann (1970) is followed here: I = interal lobe, U = umbilical lobe, L = lateral lobe, E = external lobe. Where necessary, however, Ruzhentsev's (1949, 1957) terminology is also given.

DISCUSSION

Failure to recognize the wide range of intraspecific variation in members of the ammonite family Placenticeratidae, combined with the effects of dimorphism and an extremely slow rate of evolutionary change in many lineages, has resulted in a large number of specific and generic names and concomitant taxonomic confusion. During the last decade, placenticeratids have been distributed over two subfamilies and about two dozen genera. Most of this taxonomic confusion has been cleared by Kennedy & Wright (1983) in their pioneering study of *Placenticeras polyopsis* (Dujardin, 1837). The Zululand representatives of this family, *Placenticeras kaffrarium* Etheridge, 1904, and *Hoplitoplacenticeras howarthi* Collignon, 1970, especially the former, display the above-mentioned features admirably, and permit detailed description as well as discussion on the systematics of the family supplementary to the studies of Kennedy & Wright (1983). Study of this material, as well as a review of the literature, point to several problem areas in the taxonomy of the family. These include:

1. Separation of Placenticeratidae and Engonoceratidae is by no means as clear as some authors would suggest. This problem is discussed in a separate chapter dealing with the taxonomic affinities of the genus *Hypengonoceras* (see p. 361).
2. The origin of the Placenticeratidae is clearly in the Hoplitidae, but the exact phylogeny of the group is not yet quite clear.
3. The role of sutural ontogeny in interpreting the phylogeny and its taxonomic value is disputable.
4. The validity of the numerous generic names applied to the Placenticeratidae has been dealt with by Kennedy & Wright (1983) and we can merely add some more detail on the basis of the rich Zululand faunas.
5. The validity of the numerous species referred to the family, 130 of which are listed in this study. This large number of specific names reflects, we believe, the wide range of intraspecific variation in this group. It is necessary to try to define how variable the species are and whether factors can be identified that influence

the variation. Without access to the original material no attempt is made at compiling a full synonymy of all these 'species'.

Starting at specific level, these problems can be discussed.

INTRASPECIFIC VARIATION

The fact that placenticeratid species are highly variable was already known almost 150 years ago. Dujardin (1837: 232) in his description of *Ammonites polyopsis* already commented 'Cette ammonite varie tellement, que des échantillons isolés pourraient être pris pour des espèces distinctes, si l'on n'observait quelquefois toutes les variations possibles sur les différents points d'un même échantillon'.

The most comprehensive discussion on the subject is surely provided by Hyatt (1903), who, if one reads between the lines, was very close to the truth in terms of current interpretation of variation in the group. Some of his comments are well worth quoting:

'The species of this genus (*Placenticeras*) could be readily distinguished if it were not for the great range of form in the gerontic stage, which occurs in dwarfed as well as in large specimens, and is continually mistaken for the ephebic stage.'

'The species are all connected so closely by intermediate forms that distinct lines are difficult to draw between contiguous species . . . are senile forms in the phylum, or what I have named phylogerontic. They are not scaphitoid. . . .'

'There is no real line between *P. guadalupae*, *sancarlosense*, and *planum*, nor between *newberryi* and *guadalupae*, nor between *guadalupae*, *sancarlosense*, *syrtale*, *intercalare*, and *placenta*, nor between *intercalare*, *stantoni*, *pseudoplacenta*, and *whitfieldi*. As a matter of fact there is no real break, such as is usually supposed to establish a species, between *P. guadalupae* and the extreme form of *whitfieldi*.'

'If, however, one admits that all American forms make up only one species, it becomes illogical to separate the European forms from each other or the American from them, and, consequently, all the forms of *Placenticeras* are one species.'

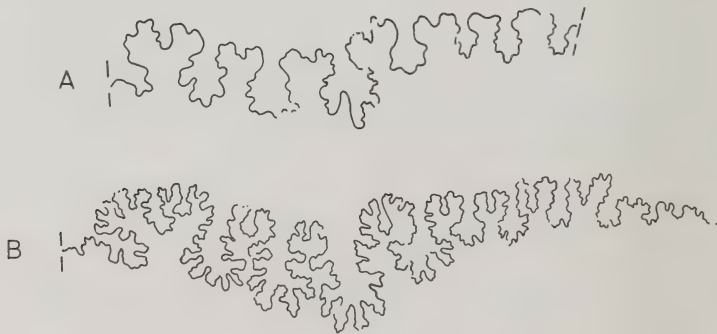


Fig. 1. Comparison of suture lines to illustrate relative size of lateral lobes. A. *Gissarites kysylchense*. B. *Placenticeras placenta*. (After Iljin 1958, fig. 2.)

Other comments on the wide intraspecific variation in placenticeratids are found widely scattered in the literature, e.g. Paulcke (1907), Reeside (1927*b*), Howarth (1965), Wolleben (1967), Summesberger (1979), Klinger & Kennedy (1980*b*, 1980*c*), Kennedy & Wright (1983), and Kennedy (1984).

It remains, however, to define this variation, or at least to try to determine which factors influence the gross morphology of the shell. Studies on the South African material and others, e.g. Summesberger (1979), Kennedy & Wright (1983), and Kennedy (1984), show that the following factors are of importance in interpreting intraspecific variation:

1. Dimorphism.
2. Ontogenetic changes.
3. Differing rates of development giving individuals of the same size but at a different point in ontogeny, different ornament; a result of size dimorphism and of variation of adult size in individual dimorphs.
4. Variation in relative proportions and ornament, i.e. intraspecific variation *per se* at the same ontogenetic stage.
5. Phylogenetic change.
6. Geographic variation.

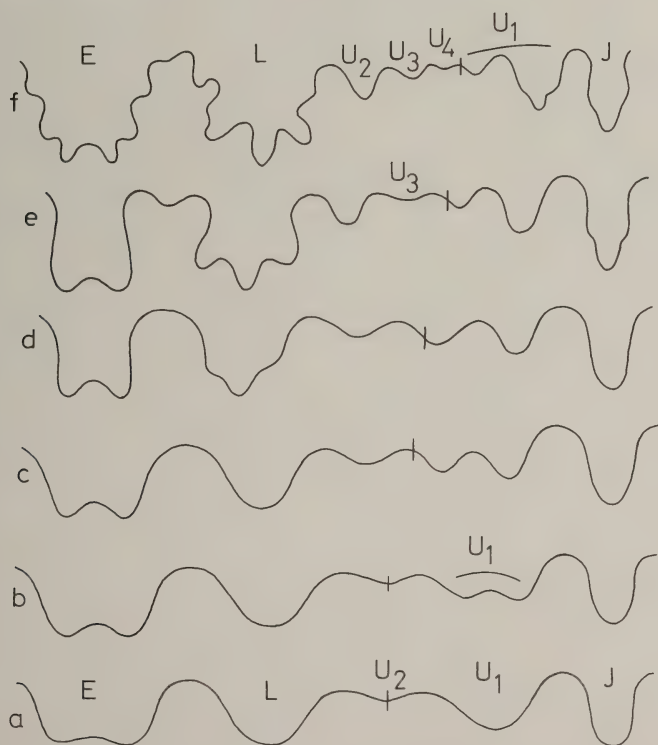


Fig. 2. Sutural ontogeny of *Metaplacenticeras pacificum* (Smith, 1900). (After Smith 1900, pls 27-28.)

DIMORPHISM, ONTOGENETIC CHANGES AND DIFFERING RATES OF DEVELOPMENT

These three factors are intimately linked and it is impossible to separate them entirely in this discussion. Ontogenetic changes in placenticeratids are striking. In most *Placenticerases*, the following can be observed:

(a) *Juvenile stage*. This includes the very early stage with the protoconch, nepionic constriction, and subsequent early whorls (e.g. Hyatt 1903, pl. 43 (fig. 6)). The protoconch is globular, wider than high. It is succeeded by depressed, reniform, early whorls (Figs 9–10). Thereafter the whorls soon become compressed.

(b) *Early phragmocone stage*. Here the whorl section is distinctly compressed, much higher than wide with maximum breadth at the umbilical shoulder (Fig. 11). The flanks are smooth, save for fine sinuous, or sickle-shaped striae and growth lines. The curve of the sickle may be slightly stronger than the haft, producing feeble crescentic ribs or riblets on the outer half of the flanks (e.g. Hyatt 1903,

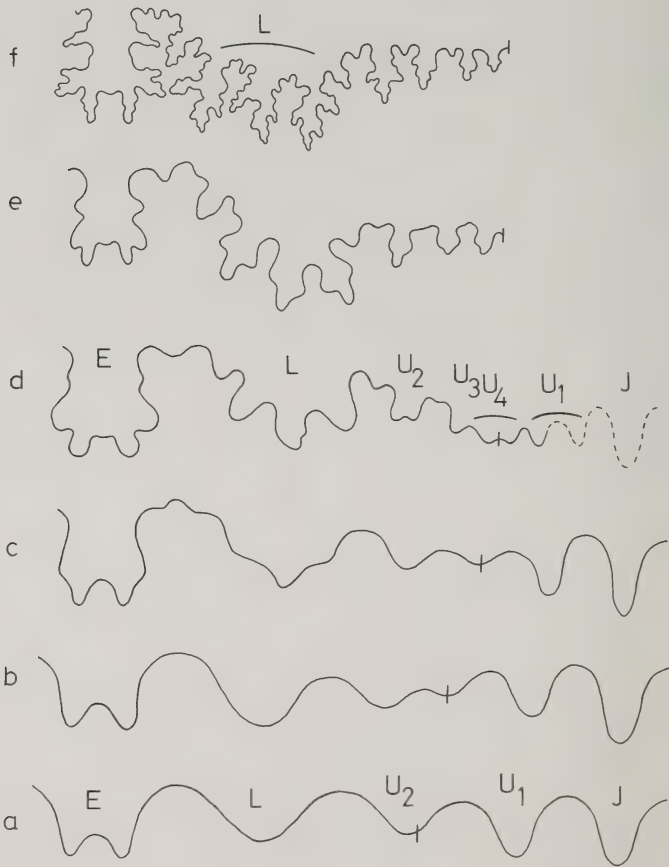


Fig. 3. Sutural ontogeny of *Metaplacenticeras pacificum* (Smith, 1900). (After Smith 1900, pls 27–28.)

pl. 43 (figs 7–8)). The venter is concave to flat and smooth, bordered on either side by entire, sharp ventrolateral edges. The umbilicus is narrow and funnel-shaped with a sharp umbilical shoulder.

(c) *Middle to early/late phragmocone stage*. Here the whorl section becomes more inflated and rounded, the umbilical shoulder becomes more rounded, and umbilical tubercles may be connected by single or bifurcating ribs of varying strength to weak or prominent lateral tubercles. Concomitantly, the venter becomes tabulate, usually with distinct alternating clavi. Ventral clavi and umbilical tubercles generally appear simultaneously (Figs 12–13).

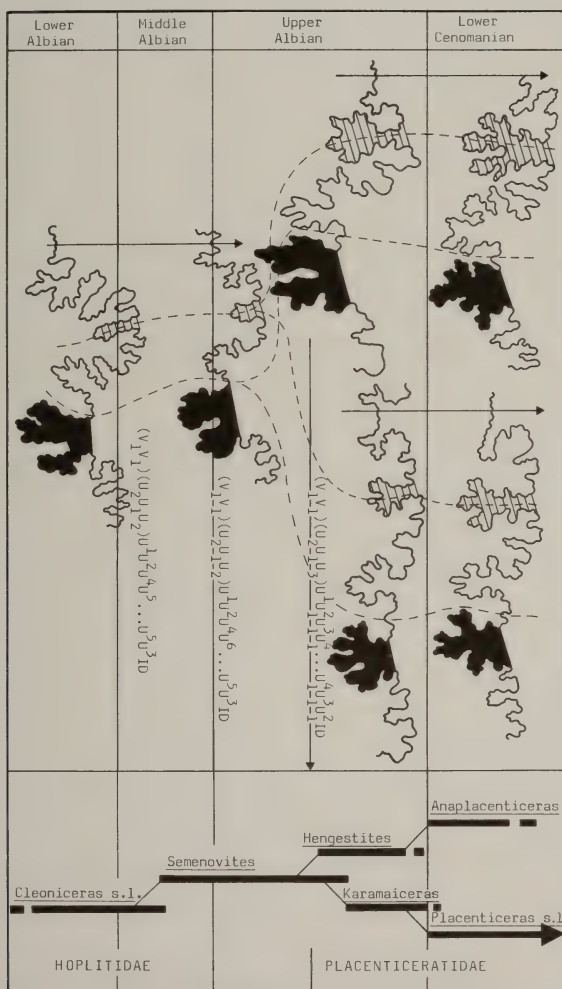


Fig. 4. Phylogeny and sutural development of Placenticeratidae from Hoplitidae. (After Mirzoev 1967, fig. 5.)

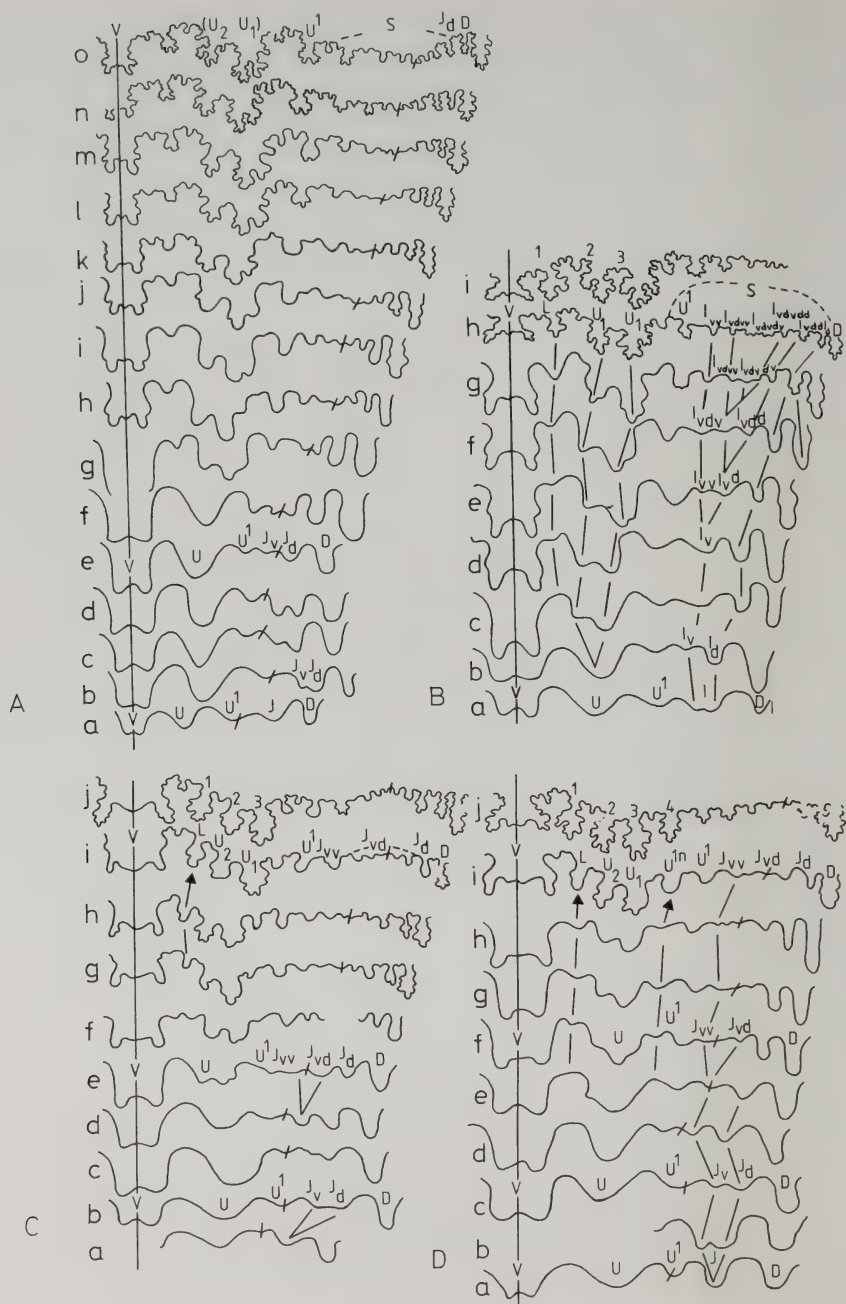


Fig. 5. Sutural ontogeny. A. *Anahoplites michalski*. B. *Kopetdagites grossouvrei*. C. *Beschubites beschubensis*. D. *Placenticeras pitniakense*. (After Michailova 1978, fig. 1.)

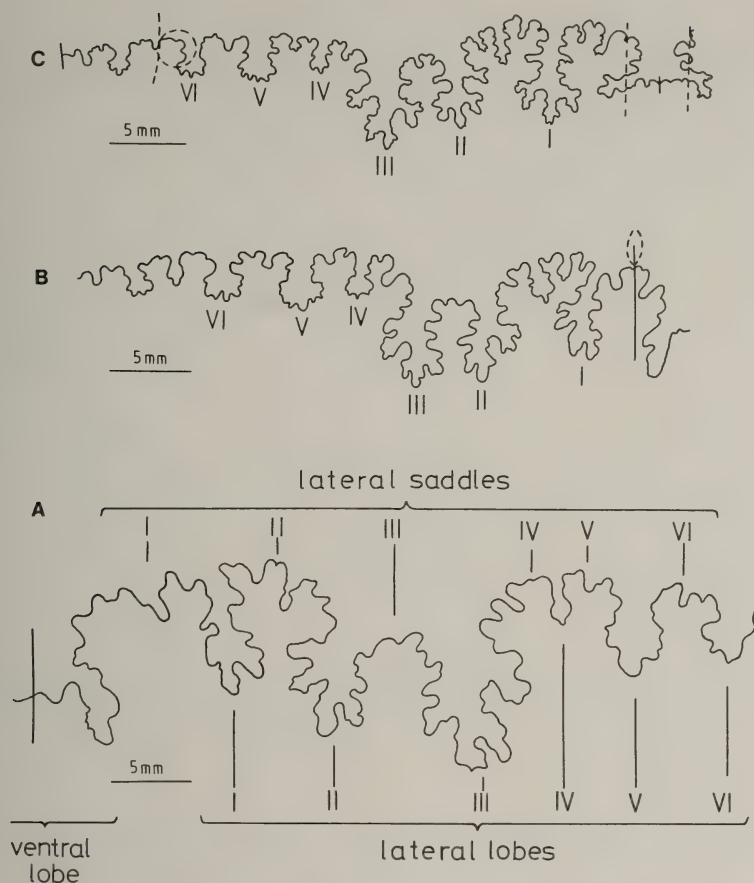


Fig. 6. Morphographic terminology applied to sutures in placenticeratids. A. *Karamaites grossouvrei* (Semenov, 1899). B. *Karamaites gaurdakense* (Luppov, 1963). C. *Karamaites mediasiaticum* (Luppov, 1963). (After Marcinowski 1980, fig. 13.)

(d) *Late phragmocone and body chamber stage*. Here the whorl section becomes even more inflated and rounded, the umbilical tubercles (if present) may migrate outward, in some up to midflank, and the venter becomes distinctly rounded and eventually may be completely smooth on the body chamber with no ventral clavi, if these were present initially. In addition, the umbilical seam egresses and part of the body chamber may show slight scaphitoid uncoiling (e.g. Hyatt 1903, pl. 32; herein Figs 12–13).

This generalized sequence of ontogenetic change can be recognized in most species of *Placenticer*, including the Zululand material, with minor deviations. It is important to note that *the rate and duration of each ontogenetic stage is*

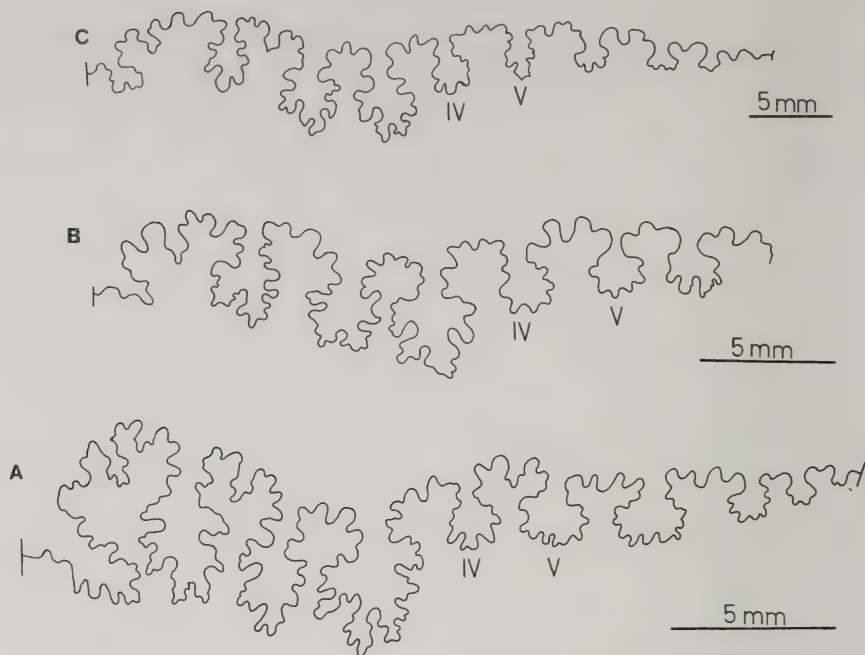


Fig. 7. Variation in size of fourth and fifth lateral lobes. A. *Karamaites kutuzovae* (Iljin, 1975). B. *Proplacenticeras planum* Iljin, 1975. C. *Placenticeras luppovi* Iljin, 1975. (After Marcinowski 1980, fig. 14.)

extremely variable. This is especially true of the two middle growth stages. After the juvenile stage, which, naturally, is present in all species, the shell may pass through all three successive stages to maturity. In others, however, the smooth, early phragmocone stage is retained to maturity, without a tuberculate stage, or the smooth stage may be very short, resulting in forms with strong tubercles and ribbing at very small diameters.

In summary, part of the difficulty in unravelling the systematics of Placenticeratidae lies in the fact that ontogenetic changes occur at different rates in different individuals of the same species, while others may omit later developmental stages. As a result, assemblages can include adult forms with the same ornament as juveniles, as well as individuals where late typically phragmocone modifications already occur at very early growth stages of some forms. In rare cases, an ontogenetic stage can even be omitted.

Dimorphism in *Placenticeras*, more specifically *P. polyopsis* (Dujardin, 1837), was demonstrated by Summesberger (1979) (as *Stantonoceras depressum* (Hyatt)) and Kennedy & Wright (1983). Until quite recently, recognition of dimorphism was mainly restricted to pre-Cretaceous ammonites (e.g. Makowski 1962; Callomon 1963, 1981), the notable exception being the Late Cretaceous scaphitids (Cobban 1969). Only in recent years has dimorphism been recognized

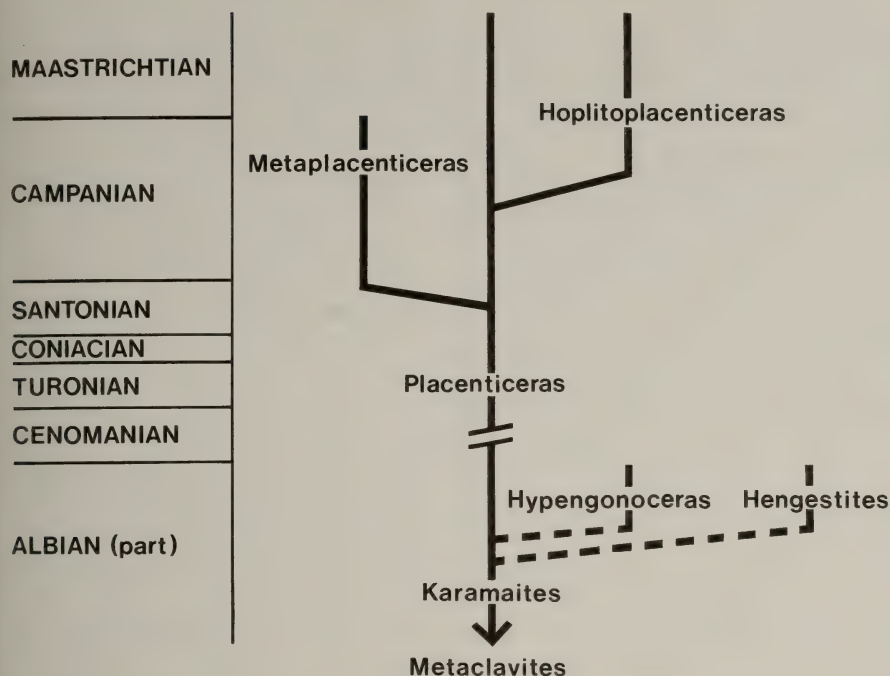


Fig. 8. Phylogeny of Placenticeratidae. (After Kennedy & Wright 1983, text-fig. 5.)

in Cretaceous forms and Kennedy & Wright (1985) now claim to have recognized it in all but three Upper Cretaceous families. Dimorphism in Cretaceous taxa is mainly limited to differences in relative adult size (see especially Callomon (1981: 269–270) on the Albian species described by Scholz (1979) as *Pervinquieria* (*Subschloenbachia*) *rostrata* and *Hysterocheras* (*Cantabrigites*) *cantabrigense*). For recent discussion see Kennedy & Wright (1985).

Unequivocal dimorphic pairs can only be recognized in adult individuals. Criteria for recognizing adult specimens as applied mainly to Jurassic forms (*cf.* Makowski 1962; Kennedy & Cobban 1976) include:

1. Slowing of growth, indicated by crowding and often interference of later septa and/or simplification of the sutures.
2. Changes in ornament on the body chamber—either attenuation of the strong ornament found on the phragmocone, or appearance of strong ornament on the body chamber following weak ornament on the phragmocone. The former commonly characterizes macroconchs, the latter microconchs.
3. Egression of the umbilical seam, leading to a slight scaphitoid uncoiling of the body chamber.
4. Apertural modifications.

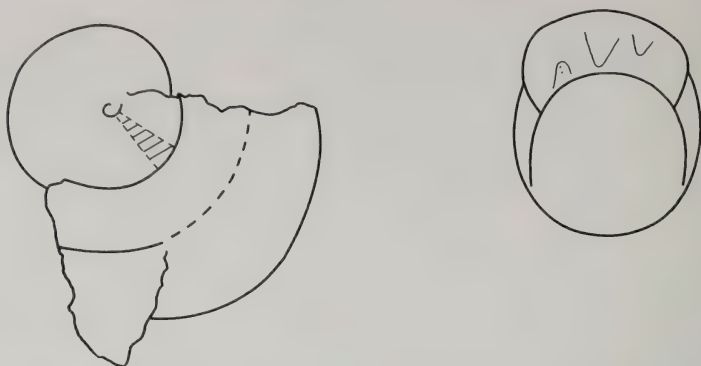


Fig. 9. *Placenticeras kaffrarium* Etheridge, 1904. Protoconch and early whorls. Note nepionic constriction. NMB D941/7. $\times 25$.

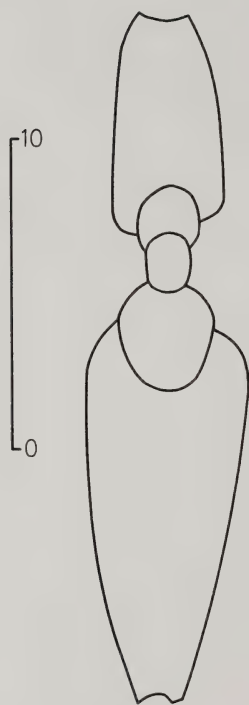


Fig. 10. *Placenticeras kaffrarium* Etheridge, 1904. Early ontogeny of whorls up to '*P. umkwelanense*' stage. Unregistered specimen. Scale bar in mm.

Some of these criteria are difficult to apply to placenticeratids. The septa in most placenticeratids are already closely spaced in early parts of the phragmocone, and interference of sutures is by no means restricted to the terminal stages of growth. Apertural modifications are difficult to recognize in this family, because complete apertures are rarely preserved. To our knowledge, the only complete *Placenticeras* aperture was recorded by Vredenburg (1907); we have but a single questionable example from Zululand (Fig. 14A).

Instead, egression of the umbilical seam and consequent scaphitoid uncoiling of the body chamber, changes in the whorl section, and modifications of ornament are much better indicators of maturity. Scaphitoid uncoiling of the body chamber can be very obvious (e.g. Hyatt 1903, pl. 32), so much so that Chiplonkar & Ghare (1977a) even erected a new genus *Placentoscaphtes* within the family Scaphitidae for what are in part mere *Placenticeras* adults with uncoiled body chamber. This uncoiling of the body chamber is accompanied by rounding of the venter and loss of ventral clavi. In addition, the umbilical wall and shoulder flatten, the umbilical diameter increases, and the umbilical edge becomes rounded towards and on the body chamber. In some forms with strong ornament, the umbilical tubercles migrate away from the umbilical edge towards maturity and weaken, or even disappear. Conversely, forms with smooth phragmocones may suddenly develop weak umbilical and lateral ornament on the body chamber (Fig. 46).

The manifestations of dimorphism in placenticeratids are complex, and not as simple as implied by Kennedy & Wright (1983). The general trend seems to be that in the early (Albian and Cenomanian) forms, such as '*Karamaites*', dimorphism is mainly restricted to size, whereas later forms, e.g. Santonian *Placenticeras polyopsis* (Dujardin), have strongly differentiated dimorphic pairs, with microconchs having much stronger ornament at smaller diameters, whereas macroconchs retain the smooth or weakly ornamented stage to much greater diameters and are generally weaker ornamented at maturity than their microconch counterpart (i.e. *Stantonoceras* vs *Placenticeras*). Partly because of this, Kennedy & Wright (1983: 868) decided to retain *Karamaites* as a separate taxon, indicating, however, that should subsequent investigations show *Karamaites* to have strongly differentiated dimorphs, it should be reduced to a synonym of *Placenticeras*.

Recent work by Seyed-Emami *et al.* (1984) suggests that some early (Middle Cenomanian) placenticeratids are already strongly dimorphic. *Karamaites grossouvrei* (Semenov, 1899), which may reach diameters of up to half a metre, and the very closely allied if not conspecific *Karamaites mediasiaticum* (Luppov, 1963), with weak lateral ornament and compressed whorl section, occur together with the smaller, strongly ornamented *Karamaites gaurdakense* (Luppov, 1963). Middle Coniacian *Placenticeras kaffrarium* from Zululand also show distinct dimorphic pairs, macroconchs retaining weaker ornament to greater diameters than the strongly ornamented microconchs. However, distinct dimorphic pairs that differ only in terms of relative size also occur. Thus dimorphism in itself is a

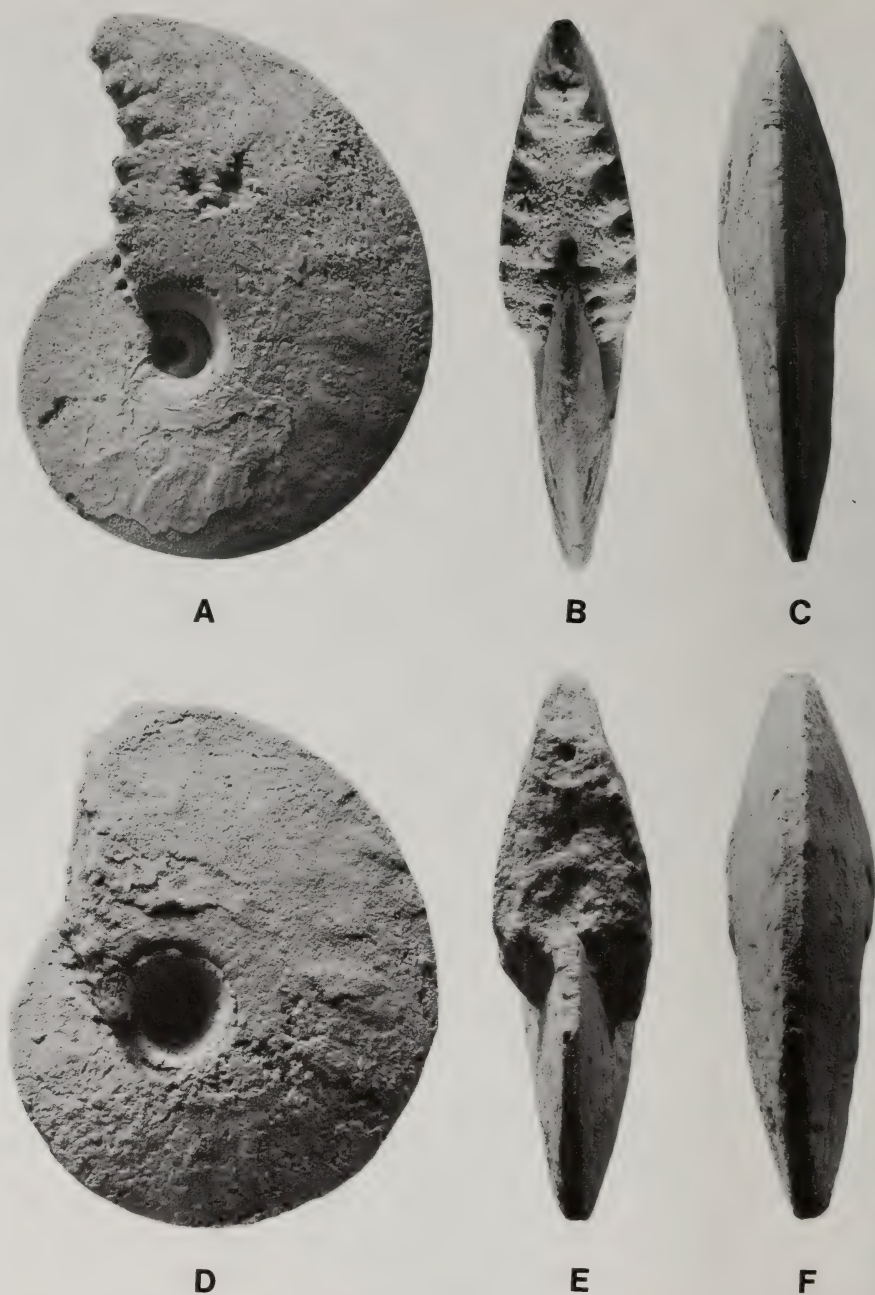


Fig. 11. *Placenticerus kaffrarium* Etheridge, 1904. A-C. SAS Z1520. D-F. NMB D941/48. Specimens showing compressed, smooth early phragmocone 'umkwelanense' stage. Note slight falcoid swellings on flanks.



Fig. 12. *Placenticerus kaffrarium* Etheridge, 1904. SAM-PCZ6194. Macroconch showing distinct ontogenetic changes from '*umkwelanense*' through '*subkaffrarium*' to adult '*kaffrarium*' stage. $\times 0.7$.



Fig. 13. *Placenticerus kaffrarium* Etheridge, 1904. SAM-PCZ6194. Macroconch showing distinct ontogenetic changes from 'umkwelanense' through 'subkaffrarium' to adult 'kaffrarium' stage. $\times 0,7$.



Fig. 14. *Placenticerus kaffrarium* Etheridge, 1904. SAS Z1081. Microconch with possible aperture preserved. $\times 1$. B. *Hoploplacenticerus howarthi* Collignon, 1970. NMB D1314. Microconch. $\times 1$.

difficult criterion to apply for generic separation and, on that basis alone, *Karamaites* does not bear separation from *Placenticerias*.

There is thus a distinctive trend in the nature of dimorphism in placenticeratids from size alone, to size and differences in strength of ornament. Ornament-related dimorphism becomes obvious only when distinct lateral ornament, especially lateral tubercles, developed—on present evidence, mainly during the Turonian and Coniacian. At present it is not possible to pinpoint the stage at which size related dimorphism gave way to ornament- and size-related dimorphism. In any case, the transition is gradual and cannot be used as a basis for generic and subgeneric division of the groups.

VARIATION IN RELATIVE PROPORTIONS

Intraspecific variation in the strict sense is difficult to separate satisfactorily from the other variable factors, unless dealing with adult specimens. In immature phragmocones one is never sure if differences in ornamentation are due to simple intraspecific variation or because specimens are at a different ontogenetic stage. In the Zululand specimens very conspicuous differences are found in the whorl sections of specimens from the same restricted stratigraphic levels but with more or less the same type of ornament. Thus the ratio of whorl breadth to whorl height appears to be in part independent of ontogenetic change, and part of true intraspecific variation. Intraspecific variation in the adult stage is very obvious, as far as ornament is concerned, as is reflected by the multitude of names in current use for specimens from the same restricted stratigraphic level.

PHYLOGENETIC CHANGE

Probably the most difficult factor to understand in the systematics of Placenticeratidae is the role of phylogenetic change. Intraspecific variation and the nature and rate of ontogenetic change are far more prominent, and completely overshadow morphological changes through time. As far as coiling is concerned, Placenticeratidae are extremely conservative and are characterized by a narrowly umbilicate shell form. Apart from slight modifications on the later part of the phragmocone and on the body chamber, very little change can be detected in the coiling of the shell. Only changes in ornament take place and these are very subtle.

The earliest forms, e.g. *Karamaites* in the Upper Albian, already have umbilical tubercles, ventral clavi, and falcoid or sickle-shaped ribs at some ontogenetic stage. Initially the umbilical tubercles are the dominant element of the ornament but, gradually, feeble lateral swellings appear on the flanks at the point where the ribs bifurcate. Distinct swellings or tubercles develop mainly during the Upper Cenomanian to Lower Turonian, but are well established by the Upper Turonian. Appearance of lateral tubercles is also associated with the development of stronger ribbing. Eventually lateral ornament becomes dominant in the Coniacian, and distinct dimorphic pairs can be recognized on the basis of ornament as well as disparate size in the Coniacian. During the Santonian the

picture is less clear. In one branch of the placenticeratids there is a distinct trend towards outwards migration of the tubercles—the umbilical tubercles migrate away from the umbilical wall to a point near mid-flank, and the lateral tubercles migrate close to the ventral tubercles. In addition, there appears to be a gradual reduction in ribbing. This trend can be seen in the Santonian *Placenticerus polyopsis* (Dujardin). This branch probably gave rise to the Upper Campanian to Upper Maastrichtian *Hoplitoplacenticerus*. This genus displays as much variation as all the other placenticeratids during the whole of the stratigraphic range of the family. At the same time the genus *Metaplacenticerus* arose. It has approximately the same stratigraphic range as *Hoplitoplacenticerus* but is said to differ in possessing a median keel at some stage of growth. This is to be discussed below. However, *Metaplacenticerus* presumably arose from the same stock as *Hoplitoplacenticerus*.

The other branch of placenticeratid evolution is the poorly known Maastrichtian genus '*Gissarites*'. This displays a very narrow venter and apparent reversal to early *Placenticerus* ornament, consisting of conical umbilical tubercles, weak lateral nodes, and very fine external clavi. The Lower Campanian '*Diplacmoceratus bidorsatus*' perhaps occupies an intermediate position between *Placenticerus paraplunum* and '*Gissarites*' and is possibly the rootstock of '*Gissarites*'.

GEOGRAPHIC VARIATION

Another factor affecting variation may possibly be geographic distribution. With the information at our disposal, it is difficult to separate the effects of geographic isolation and possible development of subspecies and phenotypic variation related to environmental control. A prerequisite for any comparisons of this kind is precise stratigraphic control, based on taxa other than placenticeratids, unless we are to become involved in a circular argument. The only locality where such correlation with Zululand is possible is Madagascar. Judging by the Coniacian faunas from Betioky, illustrated by Collignon (1965*b*), it seems that placenticeratids are much less common there and, also, that coarsely ornamented forms of *Placenticerus kaffrarium* are absent (or at least not illustrated). It is impossible to determine whether this is due to genetic differences between what are clearly populations of the same species, or a phenotypic response to different environmental conditions.

SUTURAL ONTOGENY, PHYLOGENY AND SYSTEMATICS

Under the heading of intraspecific variation we mentioned that the Placenticeratidae, with the exception of *Hoplitoplacenticerus*, show very little morphological change over their entire stratigraphic range from the Albian to the Maastrichtian. In fact, some of the *Placenticerus* populations we have studied show as much morphological variation at a single stratigraphic level as the whole genus throughout its entire history. In part because of the relatively low systematic value of ornament, various attempts have been made to base the

Saddle incision ← Saddle division ← Intermed. type ← Lobe division
 - ? → = Lobe formation - ? →

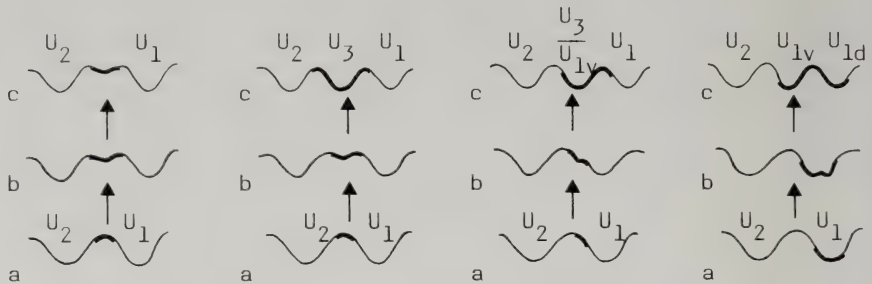


Fig. 15. Principles of lobe formation after Wiedmann (1970).

systematics of the group on details of the adult suture. Inseparable from this are attempts to use sutural ontogeny to trace the ancestry of the placenticeratids to the Hoplitidae.

Details of the sutures used in placenticeratid systematics are as follows:

1. General outline of the lobes and saddles in the adult external suture.
2. Comparative ontogenetic studies of the sutures.
3. Number of lobes and saddles in the adult external suture.

The family Placenticeratidae is one of several groups of ammonites referred to as 'Pseudoceratites of the Cretaceous' by Hyatt (1903) in his posthumous work, in which 'The complexity of the outlines of the lobes and saddles . . . is a retrogressive form that mimics to a certain extent primitive forms among Goniatitinae and Ceratitinae' (1903: 21), or, as defined by Casey (1978: 584) ' . . . ammonites characterized by simplicity of the saddles of the suture-line though with an increased number of elements'.

This type of suture line is often found associated with a narrowly umbilicate, compressed shell form. In some of the Placenticeratidae, in the sense of Kennedy & Wright (1983), the term pseudoceratitic is still applicable, but not in the majority. In *Hypenogonoceras*, which we do not regard as a placenticeratid, the saddles in the external suture generally tend to be rounded and less divided than the lobes, but not always. In all the other genera referred to the Placenticeratidae by Kennedy & Wright (1983), both saddles and lobes are finely frilled and the term 'pseudoceratitic' is a misnomer. Thus from this point of view, the family Placenticeratidae—as interpreted by Wright (1957) and Kennedy & Wright (1983)—is a heterogeneous group. This is discussed further elsewhere (see p. 361).

Unfortunately, a discussion on the comparative sutural ontogenies of the Placenticeratidae (or any other group for that matter) is very difficult, because of lack of definition of individual elements and disparate uses of terminology.

Sutural terminology is either morphological and descriptive ('morphographic') or ontogenetic. Morphological terminology is useful for communicating

Wedekind (1913)	Ruzhentsev (1949b)
E	V (ventral)
L	O (omnilateral)
	+U (umbilical s. str.)
I	D
A ₁ , A ₂ ,...	L, L ¹ ,...
U ₁	I
U _n	I ¹
U ₂ , U ₃ ,...	U ¹ , U ² ,...

Fig. 16. Comparison of sutural terminology of Wedekind (1913) and Ruzhentsev (1949). (After Wiedmann & Kullmann 1981: 224.)

data concerning the adult suture line, but even here it is severely limited by lack of precision. Casual reference to the number of lateral lobes, adventive and/or auxiliary elements in the adult external suture line generally confuses rather than clarifies.

Morphogenetic terminology, in which various elements of the suture can be homologized in ontogenetic studies, appears to be the ideal. Unfortunately there are difficulties which appear to be semantic and to a certain extent geopolitical. Two contrasting types of terminology exist: that of Wedekind (1916) is generally used by western palaeontologists, and that of Ruzhentsev (1949, 1957) is generally used by Soviet palaeontologists (see Kullmann & Wiedmann 1970; Wiedmann & Kullmann 1981; Fig. 16 herein). For reasons of clarity, summarized by Wiedmann & Kullmann (1981), we prefer the terminology of Wedekind (1916) but, given that most recent work on placenticeratid sutural ontogeny has been conducted by authors employing Ruzhentsev's terminology, both are given where possible, to avoid confusion (see e.g. Casey 1978: 585).

The early sutural ontogeny is well known for various placenticeratids (see list below), although differences of interpretation exist.

Smith 1900	<i>Metaplacenticeras pacificum</i> (Smith, 1900)
Hyatt 1903	<i>Placenticeras pseudoplacenta</i> Hyatt, 1903
	<i>Placenticeras whitfieldi</i> Hyatt, 1903
Matsumoto 1953	<i>Metaplacenticeras subtilstriatum</i> (Jimbo, 1894)
Schindewolf 1967	<i>Metaplacenticeras pacificum</i> (Smith, 1900)
Mirzoev 1967	<i>Karamaicerias kolbajense</i> Sokolov, 1965

- Iljin 1975 *Kopetdagites kopetdagensis* Iljin, 1975
 Mediasiceras beliakovae Iljin, 1975
 Beschtubeites beschubensis Iljin, 1975
 Proplacenticeras pitniakense Iljin, 1975
- Michailova 1978 *Karamaiceras kolbajense* Sokolov, 1965
 Turkmenites gaurdakensis Luppov, 1963
 Kopetdagites grossouvrei (Semenov, 1899)
 Kopetdagites sp.
 Mediasiceras saggitalis Iljin, 1975
 Beschtubeites beschubensis Iljin, 1975
 Beschtubeites kutusovae Iljin, 1975
 Placenticeras bobkovae Iljin, 1975
 Placenticeras pitniakense Iljin, 1975

Results of these investigations are unanimous in ascertaining that the primary suture is quinquelobate: E L U_2 U_1 I (Wedekind); or V U U^1 I D (Ruzhentsev). Very early in the ontogeny, the umbilical lobe U_1 (Ruzhentsev = I) divides into two elements through the process of 'Lobenspaltung' (see Wiedmann 1970: 910, fig. 1 IV) (Fig. 15), giving rise to $U_{1v}U_{1d}$ of typical hoplitid affinities, resulting in an adult sutural formula: E L U_2 U_3 (U_4 = S) $U_{1v}U_{1d}$ I (Wedekind).

Less easy to interpret (and reconcile) are: division of the lateral lobe L (Ruzhentsev U); division of the saddle E/L (Ruzhentsev V/U); and, division of the saddle L/ U_2 (Ruzhentsev U_1/U^1).

According to Mirzoev (1967) and Michailova (1974, 1978), the lateral lobe L (Ruzhentsev U) divides into two unequal parts very early in ontogeny. This bifid nature of the lateral lobe is in direct contrast to the trifid division of the same lobe in the Hoplitaceae. Soon afterwards a lobe arises in the lateral saddle E/L (Ruzhentsev V/U), which is designated L by Mirzoev and Michailova, i.e., the equivalent of A (adventive) of Wedekind. Furthermore, in *Placenticeras* s.s. a new lobe arises in the saddle L/ U_2 (Ruzhentsev— U_1/U^1), to which they apply the symbol U^{1n} (= new U^1)—in descriptive terms the fourth lateral lobe in the adult suture (Fig. 5D).

The investigations of Mirzoev and Michailova are somewhat at variance with those of Schindewolf (1967) and Kullmann & Wiedmann (1970). According to the latter, the lateral lobe L is trifid, and no mention is made of a new lobe being formed in the saddle L/ U_2 . This disparity may in part be due to differences of definition. Schindewolf (1967) had already pointed to the indiscriminate use of the term 'adventive lobe'. As per definition, an adventive lobe is a true lobe formed in the external saddle (E/L) at an early ontogenetic stage. Thus reference to 'adventitious elements' in the adult placenticeratid suture (e.g. Wright 1957;

Kennedy & Wright 1983), when in fact a tripartite division of the lateral lobe or a bipartite division of L, plus a deep incision on E/L is meant, is misleading, as Schindewolf (1967) had already commented. More difficult to resolve is the question whether the adventive lobe (Ruzhentsev—L) of Mirzoev and Michailova is in fact a true adventive lobe as per definition, or merely a deep incision of the saddle E/L. The time of formation seems to be crucial for definition. According to Schindewolf (1967: 803 (725)) the umbilical lobes are formed at an early ontogenetic stage—prior to incision of the saddles and the lobes. One would expect the same of adventive lobes.

According to Michailova (1978) the 'adventive' lobe only arises from the end of the second whorl onwards. Illustrations by Michailova (1978, fig. 1v, g) also appear to indicate that the 'adventive' lobe only really becomes prominent at a stage that coincides with the incision (Zerschlitzzung) of the other saddles and lobes. This appears to favour the idea that we are here dealing with a large incision in the E/L saddle, rather than a true adventive lobe—as also previously suggested by Smith (1900), Reeside (1926: 2), Matsumoto (1953: 146) and Schindewolf (1967: 744 (666)).

Definition of the incision of the lateral saddle E/L as an incision and not as an adventive lobe is not merely a matter of semantics or terminology, but crucial for determining phylogenetic relationships. True adventive lobes occur in the family Engonoceratidae, but not in Placenticeratidae. Wright (1957) and previously Spath (1931) had sought to derive the Placenticeratidae from Engonoceratidae—a view now generally abandoned. Furthermore, arising from study of the sutural ontogeny of the group is the problem of the systematic position of the

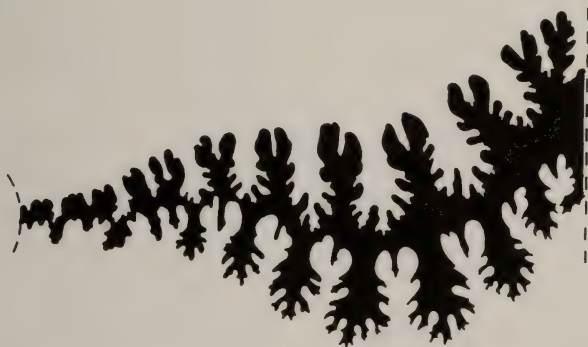


Fig. 17. Suture of *Hypengonoceras warthi* (Kossmat, 1895). (After Kossmat 1895, pl. 20 (6) (fig. 8).)

Albian genus *Hypengonoceras*, to be discussed below (see p. 361). Engonoceratidae can generally be separated quite easily from the Placenticeratidae by their ceratitic suture lines with entire or little divided saddles (Fig. 17). In some cases, however, such as the genus *Parengonoceras* Spath, 1924 (of Engonoceratidae), the sutures are finely incised, and morphological transitions to the genus *Hypengonoceras* (of Placenticeratidae as interpreted by Kennedy & Wright (1983)) occur, as demonstrated by Renz (1970). The only way to distinguish between *Parengonoceras* and *Hypengonoceras* is by means of sutural ontogeny. Unequivocal adventive lobes occur in *Parengonoceras* (Fig. 18), which clearly places the genus in the family Engonoceratidae. As yet, the sutural ontogeny of *Hypengonoceras* is unknown, and reference to the Placenticeratidae appears to be based on stratigraphic rather than phylogenetic evidence. Details of this are discussed elsewhere (p. 361). For the present it is sufficient to say that the distinguishing feature between Engonoceratidae and Placenticeratidae appears to be the presence of one or more adventive lobes in the former, as compared to a mere, albeit large, incision of the lateral saddle E/L in the latter.

The lobe in the saddle L/U₂ (fourth lateral lobe), termed U¹ⁿ by Michailova (1974, 1978), has been used as a criterion for separating genera in the Placenticeratidae. We lack material for detailed ontogenetic studies and can give no verdict on the sutural status of the lobe—whether it in fact is a real (new) lobe or merely an enlarged incision, similar to that in the external saddle; we suspect it to be the latter. Whatever the case may be, the presence, or rather the size of this 'lobe' is regarded as being of systematic value by Michailova (1978) and characteristic of the genus *Placenticerias*. In terms of descriptive terminology of the adult suture, this is the fourth lateral lobe. As summarized by Marciniowski (1980), the early (Albian–Cenomanian) placenticeratids referred to the genus *Karamaites* also have this lobe, but it is consistently smaller than the fifth lateral lobe (Figs 6–7). There is a progressive, phylogenetic increase in the size of this 'lobe' until in *Placenticerias*, in the Turonian, it exceeds the fifth lateral lobe in size. In addition, Michailova (1978) claimed that the bases of the first three lateral lobes (Ruzhentsev's L, U²U¹) widen and are bulb-like at the base, but become narrower at the neck.

An apparent final trend in sutural development of the Placenticeratidae is to be found in the Maastrichtian genus '*Gissarites*' Iljin, 1958 (Fig. 7A). Here the sixth lateral lobe is larger than the fifth, in contrast to the situation in *Placenticerias*, where the opposite holds true. In addition, the lateral branches of the external lobe E (Ruzhentsev = V) are short and blunt in contrast to paw-shaped in *Placenticerias*.

From the above it can be seen that details of the suture line are of rather ambiguous value in the systematics of the Placenticeratidae, especially at generic level.

Detailed studies of the sutural ontogeny, however, point unambiguously to the origins of Placenticeratidae in Hoplitidae. Salfeld (1924) and Matsumoto (1953) tried to trace the origins of Placenticeratidae back to the Phylloceratidae.

Salfeld based his conclusions on incorrect sutural data from the type species of *Hypophylloceras*, as shown subsequently by Wiedmann (1962: 248). Matsumoto based his findings on supposed affinities of the juvenile shells of *Metaplacenticeras subtilstriatum* and *Phylloceras*, and also claimed that the sutures of *Metaplacenticeras* were somewhat phylloid—analogueous to those of *Neophylloceras*. Also, the fact that the siphuncle only reached its marginal position towards the end of the second whorl was claimed to be a phylloceratid feature. Spath (1930) and Wright (1957: L109, L390) tried to derive the Placenticeratidae from the Engonoceratidae, but the reasons for this are now seen as a combination of homoeomorphy and stratigraphic 'neatness' rather than actual relationship. It is now generally accepted that the origin of Placenticeratidae lies in the Hoplitidae—a theory dating back to Douvillé (1890), and followed by Kossmat (1897), Smith (1900), De Grossouvre (1894), Pervinquière (1907) and others.

Casey (1965: 461) suggested that early placenticeratids, such as *Hengestites* Casey, 1960, *Anaplacenticeras* Iljin, 1959, and *Karamaites* Sokolov, 1965, arose from the hoplitid *Semenovites* Glazunova, 1960. Schindewolf (1967) summarized alleged phylogenetic relationships of Placenticeratidae and confirmed that the origins must lie in the Hoplitidae. Mirzoev (1967) undertook detailed studies of *Cleoniceras*, *Semenovites* and '*Karamaiceras*', and substantiated the derivation of Placenticeratidae from Hoplitidae via subfamily Semenovitinae Mirzoev, 1967, the latter consisting of the two genera *Semenovites* Glazunova, 1960, and

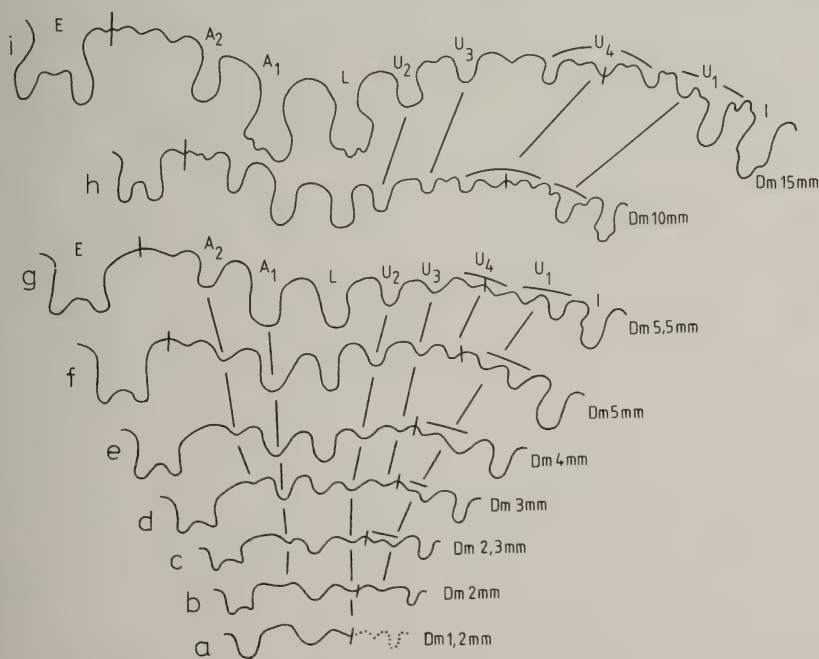


Fig. 18. Sutural ontogeny of *Parengonoceras discoides* Renz. (After Renz 1970, fig. 2.)

Metaclavites Casey, 1965 (see Fig. 4). It is significant that in the transition from Hoplitidae to Placenticeratidae as demonstrated by Mirzoev, no significant change in the form of the shell or in the degree of involution took place. Major changes affected the suture line. The lateral lobe (L) (Ruzhentsev = U) changes from asymmetrically trifold to bifid, and almost separated into two independent lobes. Simultaneously, an incision arose in the first lateral saddle, separating it almost as far as the base and the external lobe (Ruzhentsev = V) becomes shallower. This all led to the typical 'sagging' suture line of Placenticeratidae.

Derivation of Placenticeratidae from Hoplitidae was further confirmed by the detailed sutural studies of Michailova (1974, 1978), who derived '*Karamaiceras*' from the Late Albian *Anahoplites*. In addition, she also listed the sutural characteristics of the family as discussed above. These views were accepted by Casey (1978).

Kennedy & Wright (1983) derived the mainstream of Placenticeratidae—*Karamaites* and *Placenticeras*—from *Metaclavites* (Fig. 8) and tentatively regarded *Hypengonoceras* and *Hengestites* as early, parallel offshoots derived from *Karamaites* in the Albian. For reasons discussed below (p. 361), we prefer to allocate *Hypengonoceras* to the family Engonoceratidae. This only leaves us with the moot question of the systematic position of *Hengestites*. Unfortunately, we have no additional material for meaningful discussion. As far as ontogenetic development of ornament is concerned, *Hengestites* deviates distinctly from the normal placenticeratid pattern. In *Hengestites* the ornamented stage with alternating ventral clavi and lateral riblets precedes the smooth compressed stage with entire venter; in *Placenticeras* the inner whorls are smooth with entire venter and may be succeeded by an ornamented stage on the outer whorls, i.e. the complete opposite. Removal of *Hengestites* from Placenticeratidae can only be seen as a suggestion, pending detailed examination of the sutural ontogeny.

SYSTEMATIC PALAEOONTOLOGY

Phylum MOLLUSCA Cuvier, 1797

Class CEPHALOPODA Cuvier, 1797

Order AMMONOIDEA Zittel, 1884

Suborder AMMONITINA Hyatt, 1889

Superfamily HOPLITACEAE Douvillé, 1890

Family **Placenticeratidae** Hyatt, 1900

(= Hypengonoceratidae Chiplonkar & Ghare, 1976;
Baghiceratinae Chiplonkar & Ghare, 1976)

Genus *Placenticeras* Meek, 1876

Placentoceras Meek, 1870 (*nom. oblit.*)

Diplacomoceras Hyatt, 1900

Diplacmoceras Hyatt, 1903 (illegitimate emendation of *Diplacmoceras* Hyatt, 1900)
Stantonoceras Johnson, 1903
Proplacenticeras Spath, 1926
Pseudoplacenticeras Spath, 1926
Anaplacenticeras Iljin, 1959
Gissarites Iljin, 1959
Karamaites Sokolov, 1961 (*nom. nud.*)
Parastantonoceras Collignon, 1965a
Karamaites Sokolov, 1965, in Casey, 1965
Karamaiceras Sokolov, 1967
Asiatostantonoceras Iljin, 1975
Turkmenites Iljin, 1975
Kopetdagites Iljin, 1975
Mediasiceras Iljin, 1975
Beschtubeites Iljin, 1975
Baghiceras Chiplonkar & Ghare, 1976
Malwiceras Chiplonkar & Ghare, 1976
Placentoscaphites Chiplonkar & Ghare, 1977a
Sancarlosia Chiplonkar & Ghare, 1978

Type species: Ammonites placenta DeKay, 1828, by subsequent designation by Meek (1876: 462).

Diagnosis

Extremely variable, generally compressed and involute. Earliest stages with rounded whorl section soon followed by typical compressed, high-whorled stage with crater-like umbilical pit, flat smooth flanks and smooth flat venter with sharp edges. Later stages may develop umbilical tubercles and generally ventral clavi, which are demonstrably the base of a septate spine in some; lateral sickle-shaped ribs with or without lateral thickening or tuberculation. Umbilical tubercles may or may not migrate away from umbilical edge towards maturity. At maturity, ventral clavi generally disappear, the venter becomes rounded, the umbilical wall slopes out gently and the umbilical seam egresses, leading to slight scaphitoid uncoiling of the body chamber. Variation partially caused by different rates of ontogenetic development. Strongly dimorphic; especially noticeable in forms with lateral ornament. In early forms, dimorphs differ mainly in size. Suture characteristically sagging, with saddle E/L deeply incised, and lateral lobe, L, arranged obliquely in adapical direction, whereas umbilical lobes on flanks are arranged more or less radially.

Discussion

The plethora of names listed in the generic synonymy bears testimony to the confusion in placenticeratid systematics. Kennedy & Wright (1983) placed most of these names in the synonymy of *Placenticeras*. They did, however, retain *Karamaites* Sokolov because of lack of evidence of definite dimorphism in that genus, as discussed above.

The earliest forms, '*Karamaites*' of the Upper Albian to Middle Cenomanian, are best known from Central Asia. They have ornament consisting of umbilical tubercles, falcoid ribbing and alternating ventral clavi. This includes forms such as

'*Turkmenites*', '*Kopetdagites*' and '*Mediasiceras*'. In the Upper Cenomanian *Kopetdagites*, indications of later typical *Placenticer* ornament start appearing. Small tubercles or tubercle-like swellings develop on the flanks at the point of bifurcation of the ribbing. This then leads to the typical '*Proplacenticer*' type of ornament, shown best by *P. kaffrarium*, where strongly differentiated dimorphs can be distinguished. In the Turonian to Coniacian '*Proplacenticer*', strong lateral ornament develops and in the adult stage the umbilical tubercles may migrate outwards, foreshadowing the Santonian *Placenticer polyopsis* type of ornament. Strongly ornamented microconchs correspond to Collignon's (1965a) genus *Parastantonoceras*. In later *Placenticer* species, strongly ornamented microconchs correspond to '*Stantonoceras*' or '*Asiatostantonoceras*'. *Placentiscaphites* clearly represents adult placenticeratids in which the body chamber shows signs of uncoiling, and has nothing to do with the true scaphitids whatsoever.

Of the other names included in the synonymy of *Placenticer*, *Sancarlosia* is an inflated, strongly ornamented form of *Placenticer*, probably representing microconchs, as may be *Baghiceras* and *Malwiceras*.

Gissarites (Fig. 1A) is a poorly known form from the Maastrichtian of Central Asia. It has a very narrow venter and, in many respects, resembles the early *Placenticer*, with prominent umbilical tubercles but hardly any lateral ornament. Iljin (1958) maintained that the sixth lateral lobe is larger than the fifth, by virtue of which *Gissarites* can be separated from *Placenticer*. Due to the great variation in this character, we do not believe that separation on details of the suture is advisable. Another poorly known taxon that probably does not require generic separation from *Placenticer*, is the Lower Campanian *Diplacmoceras*. This retains the entire venter to great diameters and, according to Hyatt (1903: 242), combines features of Engonoceratidae as far as ornament is concerned, but has distinct placenticeratid sutures. '*Diplacmoceras*' seems merely to be another example of juvenile ornament being retained to the adult stage and can be derived from *Placenticer paraplunum* Wiedmann of the Upper Santonian (Kennedy 1986). '*Pseudoplacenticer*' is similar to '*Diplacmoceras*'; it is known only from crushed specimens from a single locality (?Campanian) in Austria. Again, separation seems unnecessary.

Occurrence

Upper Albian to Maastrichtian, world-wide.

Placenticer kaffrarium Etheridge, 1904

Figs 9–14A, 19–20, 22–99

Placenticer kaffrarium Etheridge, 1904: 89, pl. 3 (fig. 16). Besairié, 1930: 636, pl. 64 (fig. 3–3a), suture no. 8. Venzo, 1936: 107.

Placenticer umkwelanensis Etheridge, 1904: 89, pl. 3 (figs 17–20).

Placenticer whitfieldi (auct. non Hyatt): Boule, Lemoine & Thévenin, 1907: 48, pl. 12 (fig. 5–5a). Venzo, 1936: 107, pl. 11 (fig. 12).

- Placenticerus subkaffrarium* Spath, 1921: 247, pl. 21 (fig. 2). Besairié, 1930, pl. 46 (figs 2–3).
Placenticerus cf. *subkaffrarium* Spath, 1921: 300.
Placenticerus whitefieldi [sic] Besairié, 1930, pl. 46 (fig. 1).
Placenticerus n. sp. aff. *kaffrarium* Etheridge: Venzo, 1936: 108, pl. 11 (fig. 13), text-fig. 3.
 ?*Metaplacenticerus besairiei* Collignon, 1936: 200, pl. 21 (figs 21–22).
Proplacenticerus memoriae-schloenbachi (Laube & Bruder) var. *ambiloensis* Collignon, 1965a: 14, 16, pl. 381 (fig. 1646), pl. 382 (figs 1647–1648). Chiplonkar & Ghare, 1977c: 112, fig. 6B–C.
Parastantonoceras murphyi Collignon, 1965a: 17, pl. 382 (fig. 1649).
Parastantonoceras besairiei (Collignon): Collignon, 1965a: 19, pl. 383 (fig. 1650).
Proplacenticerus stantoni Hyatt var. *bolli* Hyatt: Collignon, 1965a: 19, pl. 383 (fig. 1651).
Proplacenticerus stantoni Hyatt var. *fortior* Collignon 1965a: 19, pl. 383 (fig. 1652).
Proplacenticerus orbignyi (Geinitz): Collignon 1965a: 20, pl. 383 (figs 1653–1654).
Placenticerus reinecke Haughton, 1925: 271, pl. 13 (figs 4–5); 1926 (reprinted in French): 15, pl. 2 (figs 4–5).
 ?*Placenticerus merenskyi* Haughton, 1930: 363, pl. 11 (figs 1–3).
Proplacenticerus aff. *frütschi* de Grossouvre var. *eboroensis* Collignon, 1965b: 38, pl. 430 (figs 1780–1781).
Proplacenticerus satriense Collignon 1965b: 40, pl. 431 (fig. 1782).
Proplacenticerus nov. sp. (Venzo) aff. *kaffrarium* Ether.: Collignon, 1965b: 40, pl. 431 (fig. 1783).
 ?*Proplacenticerus merenskyi* (Haughton): Klinger, 1977, fig. 7.
Placenticerus syrtale Morton var. *tamulicum* (Blanford) Kossmat: Boule, Lemoine & Thévenin, 1907: 47 (27), pl. 12 (figs 3–4).
 ?*Proplacenticerus rampuraensis* Chiplonkar & Ghare, 1977c: 109, figs 1–2, 6A, D.
 ?*Proplacenticerus spathi* Chiplonkar & Ghare, 1977c: 110, fig. 7E, F.
 ?*Proplacenticerus frütschi* (de Grossouvre): Chiplonkar & Ghare 1977c: 113, fig. 7B–C.
 ?*Proplacenticerus stantoni* (Hyatt): Chiplonkar & Ghare, 1977c: 114.
 ?*Pseudoplacenticerus* sp. cf. *P. milleri* (Hauer): Chiplonkar & Ghare, 1977c: 115, fig. 6E–F.
Proplacenticerus stantoni (Hyatt) var. *bolli* (Hyatt): Howarth, 1985: 84, fig. 7.

Type

The holotype (Fig. 19), by monotypy, is Etheridge's original figured specimen (1904, pl. 3 (fig. 16)) from Umkwelane Hill, Zululand, housed in the Natal Museum, Pietermaritzburg, NMP 355, type number T417.

Material

Etheridge's syntypes of *Placenticerus umkwelane* (1904, pl. 3 (figs 17–20)), from Umkwelane Hill, Zululand, housed in the Natal Museum, Pietermaritzburg, NMP 453a–c, type number T418a–c. Lectotype here designated, NMP 453a (type number T418a) (Fig. 20A), the original of Etheridge's (1904, pl. 3 (fig. 17)); paralectotypes, NMP453b–c (type number T418b–c) (Fig. 20B–C). Spath's (1921, pl. 21 (fig. 2)) holotype of *Placenticerus subkaffrarium*, SAM–5106 (Fig. 21). Spath's *Placenticerus* cf. *subkaffrarium* (1921: 300), SAM–4957–4958 (Fig. 22). Several hundred specimens in the collections of the South African Museum, Cape Town; Geological Survey, Pretoria; the British Museum (Natural History), London; and University Museum, Oxford, from the following localities.

Locality 10: railway cutting, 1.1 km north of Haig Halt, Mfolozi, imprecisely located in most cases in the Coniacian.

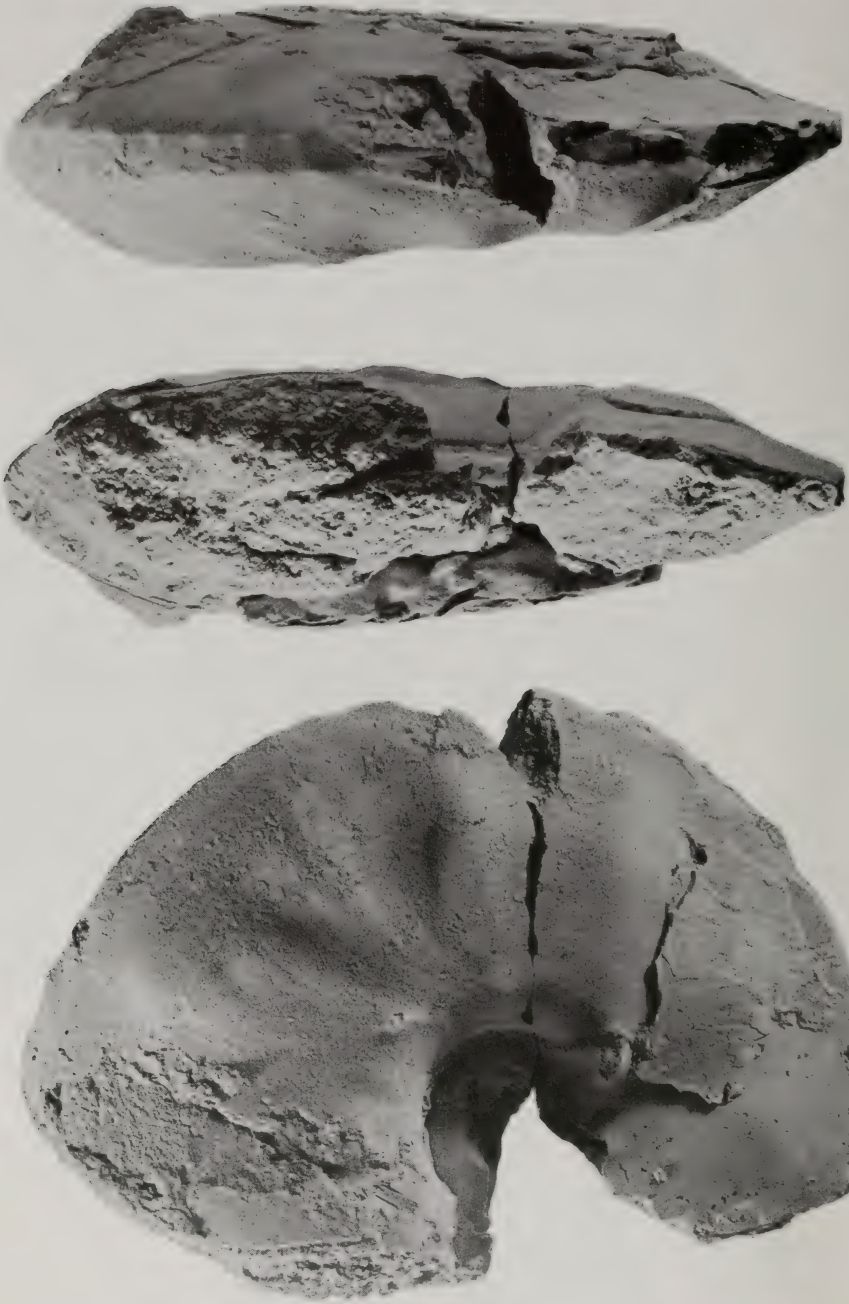


Fig. 19. The holotype of *Placeniceras kaffrarium* Etheridge, 1904. NMP 355, type number T417.

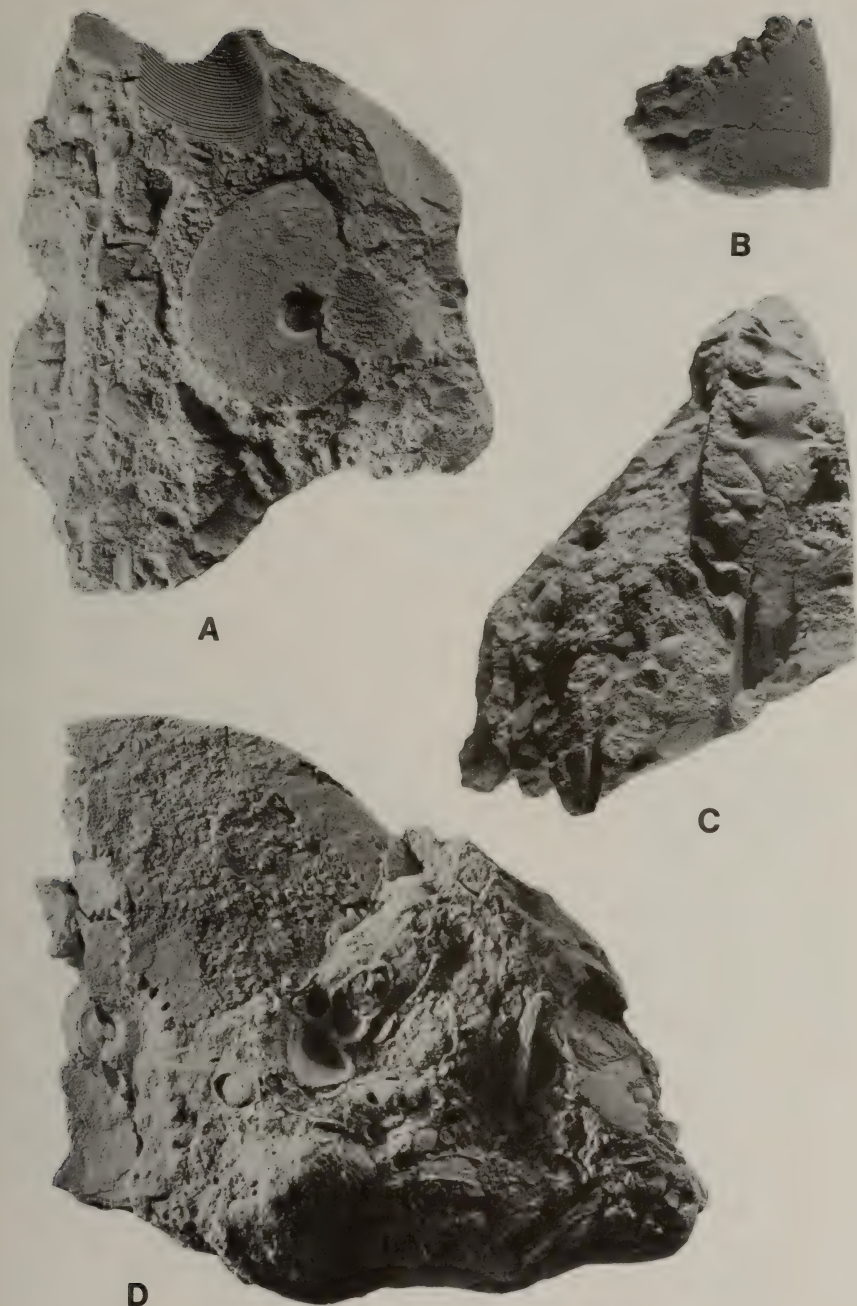


Fig. 20. *Placenticeraster kaffrarium* Etheridge, 1904. A. NMP 453a, type number T418a. The lectotype of *Placenticeraster umkwelanense* Etheridge, 1904. B-C. Paralectotypes of *Placenticeraster umkwelanense*, NMP 453b-c, type numbers T418b-c. D. SAM-PCZ6190 from locality 60, the basal *Pterotrionia* bed, Skoenberg.

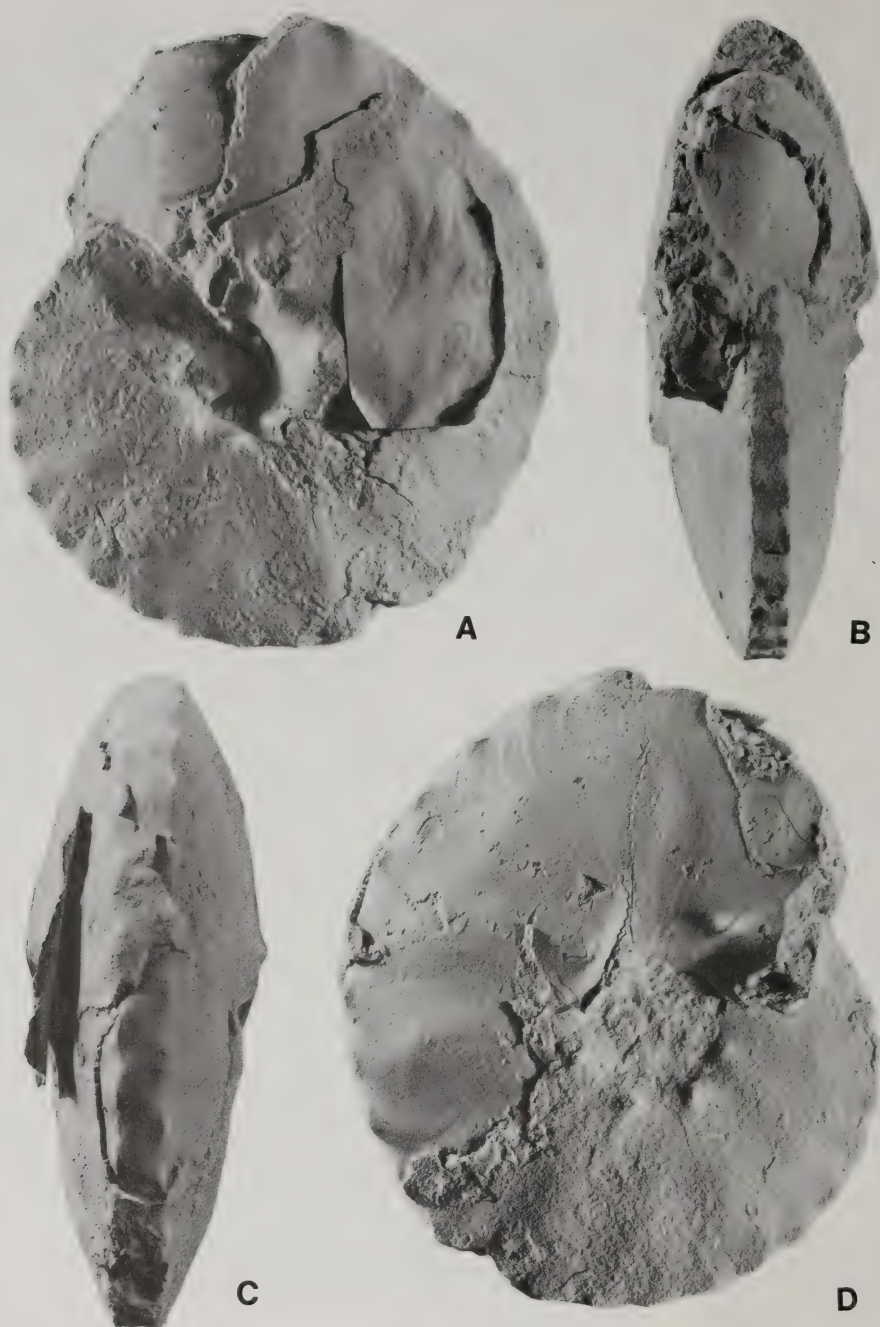


Fig. 21. The holotype of *Placenticeras subkaffrarium* Spath, 1921. SAM-5106. $\times 1$.

- Locality 11: road cut, Mfolozi. Coniacian s.l. SAM—uncatalogued and unlocalized material.
- Locality 13: hill slopes below Riverview compound, Coniacian II–III, SAS H146/3.
- Locality 16: small quarry east of track on Lot 71 13567 east of Riverview sugarmill. Coniacian II or III. SAM—uncatalogued material.
- Locality 24: cuttings and excavations for new Nyalazi River bridge. Coniacian II–V. SAS A624.
- Locality 25: cutting alongside road, 2,8 km ESE of Nyalazi River Trading Store. Coniacian II. SAM—uncatalogued and unlocalized material.
- Locality 60: basal *Pterotrigonia* Bed, Skoenberg, and overlying silts. Coniacian I. SAM–PCZ6190, PCZ6195, PCZ6200; NMB D917, D1267, D1269, D1271; SAS Z201–Z205.
- Locality 63: steep northern face of Skoenberg (Skoenberg East in Van Hoepen's catalogue), Coniacian I. NMB D941/1–51, D2846; SAS Z200.
- Locality 71: degraded river cliffs on the north bank of the Munywana Creek north of Skoenberg. Coniacian I. NMB D925/1–3, D1343–4; SAS Z252, Z401, Z1065, Z1081, Z251, Z252/1.
- Locality 72: degraded river cliffs and alluvial flats on the north side of the Mzinene, 200–300 m east of the causeway across the river. Coniacian II? and III. NMB D1148–D1150, D1151/1–15; SAS Z1028/1–3, A419, Z1125; SAM–PCZ6201, Z6202.
- Locality 92: bulldozer scrapings and adjacent hill slopes around the pumping station at the southern end of the track leading south from the farm Panplaas. Coniacian II and III. SAM–PCZ6190, Z6192, Z8205; SAS Z907, Z1442a–b, Z1520a–g, Z1603a–c, Z1063, Z1604, Z1065, Z1681.
- Locality 93: hill slopes extending on either side of the boundary fence of lots H101 and H102, Coniacian II. SAM–PCZ6187–Z6188, Z6193, Z6196–6199, Z6203–Z6204, Z6208, Z6215, Z6251–Z6255, Z6258; SAM–93B; SAS Z77, Z79, Z80, Z507, Z510, Z512, Z519, Z678, Z680, Z681, Z682, Z686, Z688, Z717, Z723, Z726, Z886, Z887, Z888, Z916, Z917, Z919, Z920, Z926, Z927, Z728, Z729, Z932, Z632, Z933, Z937, Z939, Z941, Z952, Z993, Z994, Z995, Z1003, Z1556, Z1571.
- Locality H196: on the west bank of the Hluhluwe River, at 32°19'30"E, 28°5'30"S. Coniacian II. SAM–PCZ6497.
- Locality 145: degraded bluffs on the eastern side of the Msunduzi, 3 km SW of the farm Morrisvale. Coniacian II. NMB D1184/1–26.

Over one hundred uncrushed specimens have been measured, including both juvenile and adult, microconchs and macroconchs. Rather than list these measurements in undigestible form, we have presented the data in graphic form (Figures 51–55). Lists of measurements for statistical purposes are available upon request from the Department of Invertebrate Palaeontology, South African Museum.



Fig. 22. *Placenticerus kaffrarium* Etheridge, 1904. A-C. SAM-4958. The specimen described by Spath (1921: 300) as *Placenticerus* cf. *subkaffrarium* nov. D-F. SAM-4957. The other specimen described by Spath (1921: 300) as *Placenticerus* cf. *subkaffrarium* nov. Both $\times 1$.

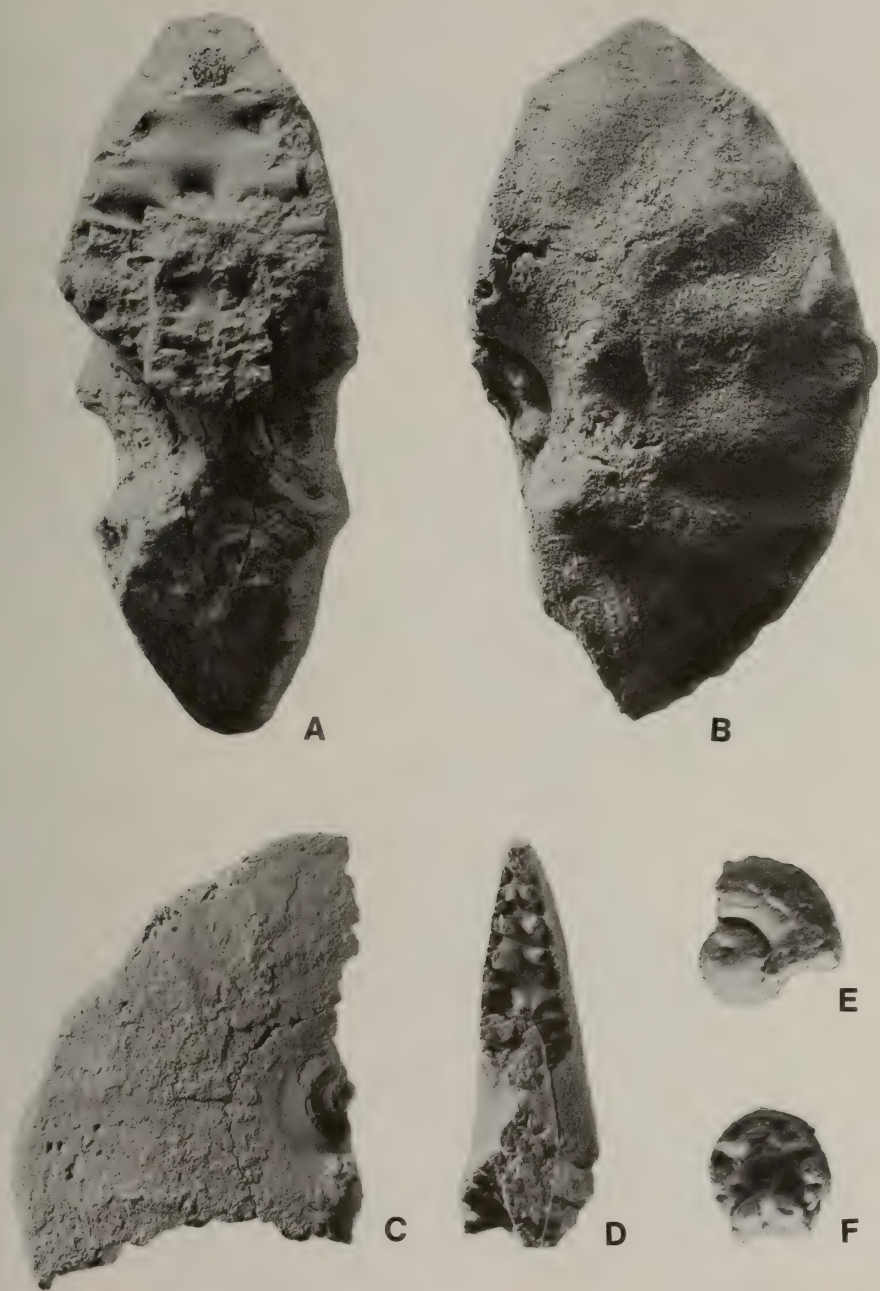


Fig. 23. *Placenticerus kaffrarium* Etheridge, 1904. Specimens showing different ontogenetic changes. A-B. NMB D917. $\times 1$. C-D. SAM-PCZ6190. $\times 1,5$. E-F. NMB D941/7. $\times 10$.

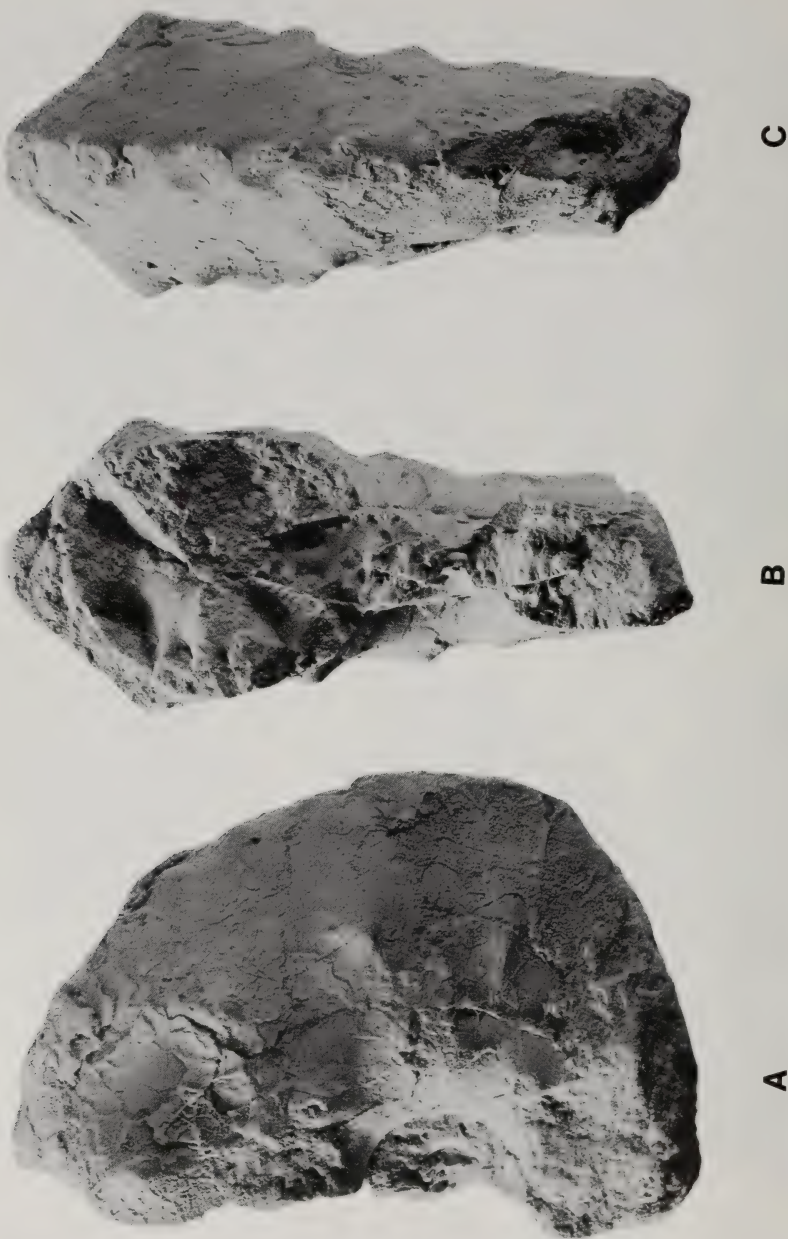


Fig. 24. *Placenticeras kaffrarium* Etheridge, 1904. NMB D1150. Microconch showing successive ontogenetic changes from rounded inner whorls, though '*umkwelanense*' and '*subkaffrarium*' stages to type 6 '*kaffrarium*' ornament. $\times 1$.

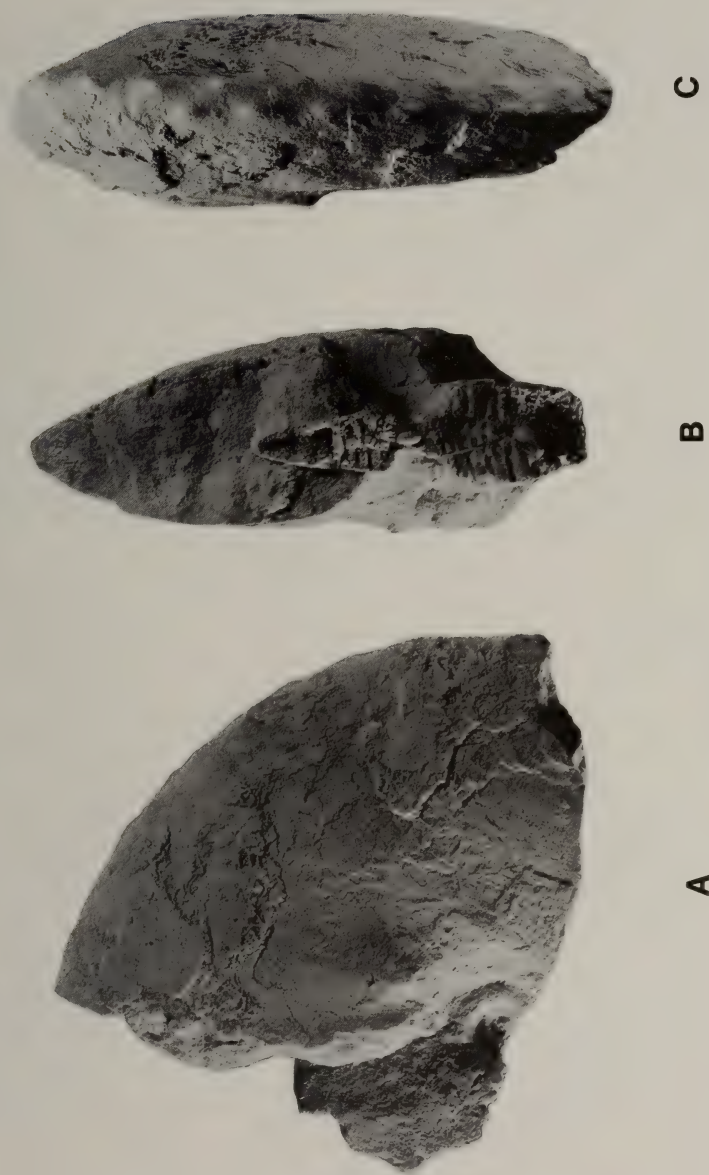


Fig. 25. *Placenticeras kaffrarium* Etheridge, 1904. NMB D1151. Specimen showing ontogenetic changes from rounded early, through compressed 'umkwelanense' to 'subkaffrarium' stage. $\times 1$.

Description

Description of the variation shown by the species is best accomplished in terms of the the following factors.

1. Ontogenetic changes

For descriptive purposes the ontogeny in typical forms can be approximately divided into four stages.

(a) *Embryonic stage*. This includes the very early stage with the protoconch and subsequent early whorls. This can be seen in NMB D941/7 (Fig. 23E-F), NMB D1150 (Fig. 24), SAS Z680, SAM-PCZ6190 (Fig. 23C-D), NMB D1151 (Fig. 25). The protoconch is globular, as wide as high, followed by depressed, reniform, early whorls. These soon become circular in cross-section at a diameter of about 2 mm. Thereafter, the whorls soon become compressed, as in typical large *Placenticeras*. The nepionic constriction can be seen in NMB D941/7 (Figs 9, 23E-F). Unfortunately most of these specimens have undergone secondary recrystallization, and details of the early sutural development are not clear, nor can the position of the siphuncle be determined accurately.

(b) *Early phragmocone stage* (Figs 11, 23C-D). Here the form is at what may be termed as the '*umkwelanense*' stage, with very compressed whorls with maximum breadth at the umbilical shoulder. The flanks are smooth, save for fine, falcoid or sickle-shaped striae. The curve of the 'sickle' may be slightly stronger than the haft, producing slight crescents on the ventral half of the flanks. The venter is concave to flat and smooth, bordered on either side by entire, sharp, narrow ventrolateral shoulders.

(c) *Middle to early-late phragmocone stage*. Here, the whorl section becomes more inflated and rounded, the umbilical shoulder also becomes more rounded, umbilical tubercles of varying strength, c. 7-8 per whorl develop, connected by single or bifurcating ribs of varying strength to weak or prominent lateral tubercles. Concomitantly, the venter becomes tuberculate with distinct alternating ventral clavi. Generally, as soon as the umbilical tubercles appear, the edges of the venter become crenulate. This is the '*subkaffrarium*' stage (Figs 26-28).

(d) *Late phragmocone and body chamber*. Here the whorl section becomes even more inflated and rounded, the umbilical tubercles migrate outwards, weaken, and the venter becomes distinctly rounded and eventually completely smooth on the body chamber. Lateral ornament may also weaken considerably towards and on the body chamber. The body chamber may also show slight egression of the umbilical seam, resulting in scaphitoid uncoiling. This is the typical '*kaffrarium*' stage (Figs 29-31).

With the exception of the embryonic stage, all these ontogenetic stages can be observed in SAM-PCZ6194 (Fig. 13), SAM-93B/4 (Fig. 32), SAS Z1080 (Figs 33-34), and SAS Z1820 (Fig. 35).

However, part of the difficulty in unravelling the systematics of the genus *Placenticeras* lies in the fact that these different ontogenetic changes occur at

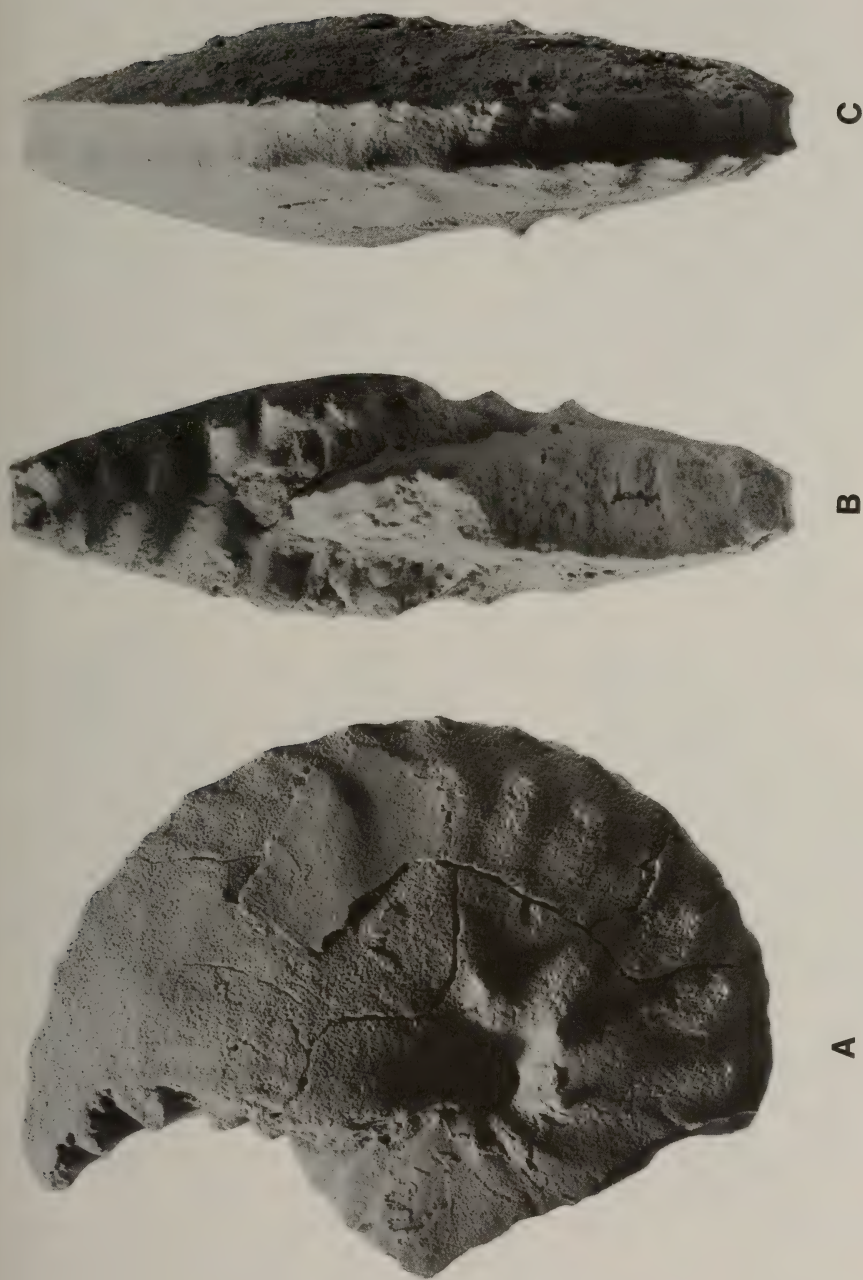


Fig. 26. *Placenticeras kaffrarium* Etheridge, 1904. SAS A499. Specimen showing typical '*subkaffrarium*' ontogenetic stage with prominent umbilical tubercles and ventral clavi, but lack of prominent lateral ornament. $\times 1$.

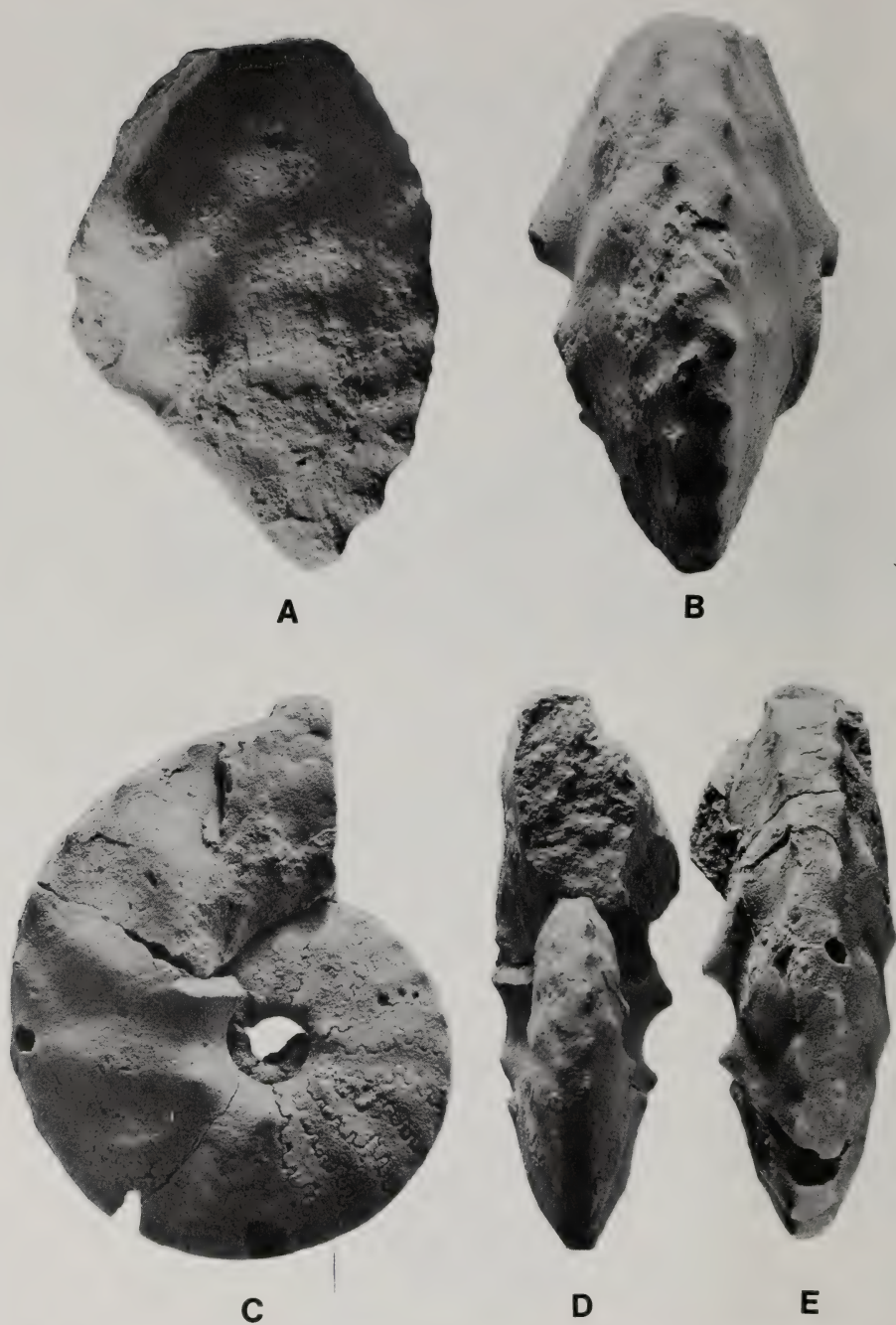


Fig. 27. *Placenticerus kaffrarium* Etheridge, 1904. A-B. SAM-PCZ6200. C-E. SAS Z682. Two specimens with 'subkaffrarium' type of ornament to illustrate variation in whorl breadth and outline. Both $\times 1$.



Fig. 28. *Placenticeras kaffrarium* Etheridge, 1904. SAS Z1028/1. Specimen showing transition from smooth 'umkwelanense' stage to 'subkaffrarium' stage with umbilical tubercles and ventral clavi. $\times 1$.

different rates, and stages are of different length in different individuals, or may be omitted. This leads to the presence of adult individuals resembling—in terms of ornament—the juveniles of others, while late phragmocone modifications already occur in the very early developmental stages of some specimens (Fig. 36), all at the same stratigraphic level (Figs 37–38). In rare cases an intermediate ontogenetic stage can even be omitted. The best way of describing this variation in ontogeny in combination with normal intraspecific variation is by illustrating the different morphotypes. This is based mainly on the presence and/or stage of appearance of the umbilical and lateral tubercles and crenulation of the venter.

2. Dimorphism

Distinct dimorphism can be distinguished in adults in these different morphotypes (see p. 251 for criteria for recognizing maturity).

(a) In all adult specimens the venter becomes rounded and generally smooth on the body chamber with no ventral clavi.

(b) In forms with strong '*kaffrarium*' or '*subkaffrarium*' type of ornament on the phragmocone, umbilical tubercles migrate away from the umbilical wall and weaken or disappear on the body chamber.



Fig. 29. *Placenticerias kaffrarium* Etheridge, 1904. SAS Z1520a. Specimen showing late phragmocone and body chamber modifications. $\times 1$.



Fig. 30. *Placenticerus kaffrarium* Etheridge, 1904. NMB D1344. Specimen showing late phragmocone and body chamber modifications. $\times 0,98$.



Fig. 31. *Placenticerias kaffrarium* Etheridge, 1904. NMB D1344. Specimen showing late phragmocone and body chamber modifications. $\times 0,75$.



Fig. 32. *Placenticerus kaffrarium* Etheridge, 1904. SAM-93B/4. Specimen showing successive ontogenetic stages. $\times 1$.



Fig. 33. *Placentiaceras kaffrarium* Etheridge, 1904. SAS Z1080. Macroconch showing successive ontogenetic changes up to body chamber. $\times 0,75$.



Fig. 34. *Placenticerias kaffrarium* Etheridge, 1904. SAS Z1080. Macroconch showing successive ontogenetic changes up to body chamber. $\times 0,75$.



Fig. 35. *Placenticerus kaffrarium* Etheridge, 1904. SAS 1820. Microconch showing distinct ontogenetic changes from 'umkwelanense' through 'subkaffrarium' to 'kaffrarium' stage. $\times 0,75$.

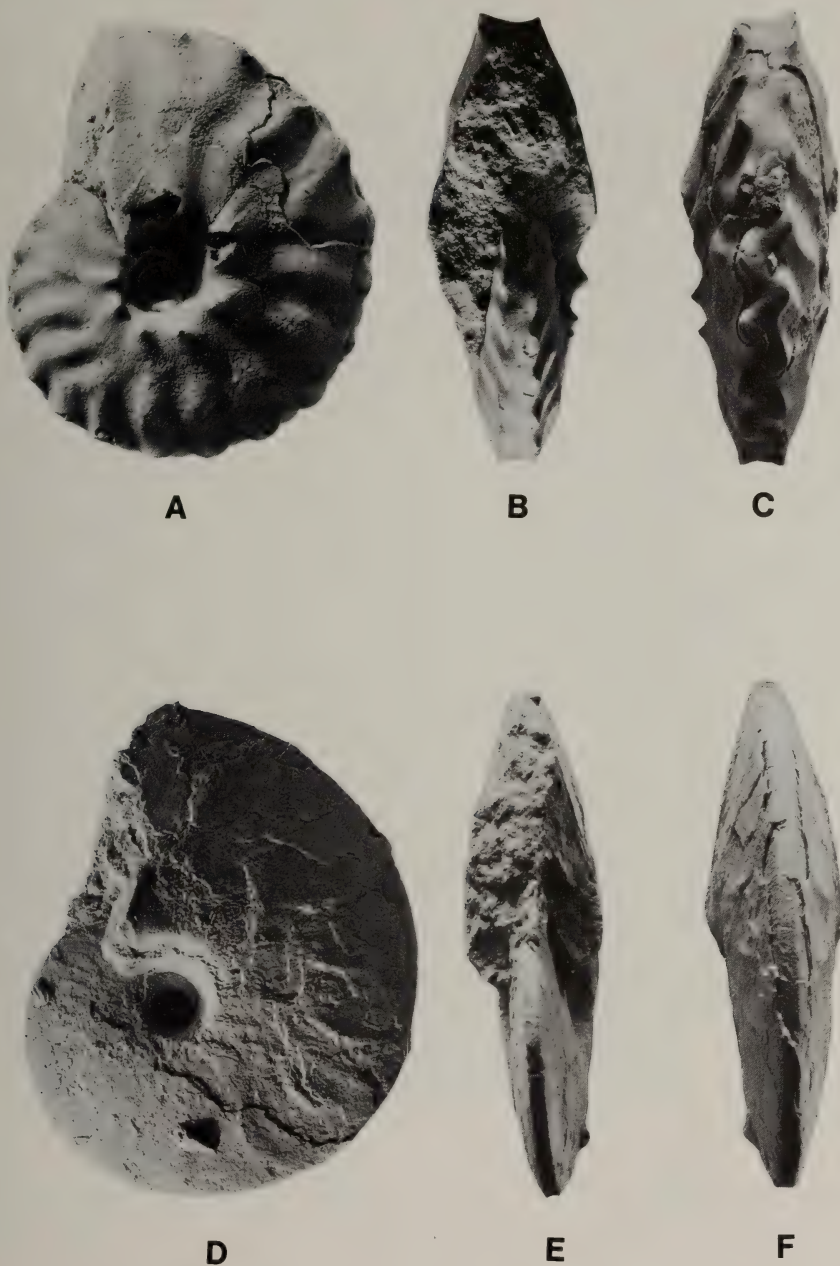


Fig. 36. *Placenticeras kaffrarium* Etheridge, 1904. A-C. NMB D2845. D-F. NMB D941/48. Both specimens at similar diameters to illustrate differing rates of ontogenetic change. The upper specimen already has the mature '*kaffrarium*' ornament, whereas the lower is still at the '*umkwelanense*' stage. Both $\times 1,5$.



Fig. 37. *Placenticerus kaffrarium* Etheridge, 1904. SAS A419. Concretion from locality 72 to illustrate the co-occurrence of '*umkwelanense*' and '*kaffrarium*' forms at the same stratigraphic level. $\times 1$.



Fig. 38. *Placenticerias kaffrarium* Etheridge, 1904. SAM, uncatalogued specimen. Concretion from locality 72 to illustrate the co-occurrence of 'umkwelanense' and 'kaffrarium' forms at the same stratigraphic level. Part of *Peroniceras* (*Zuluiceras*) at top left. $\times 0,5$.

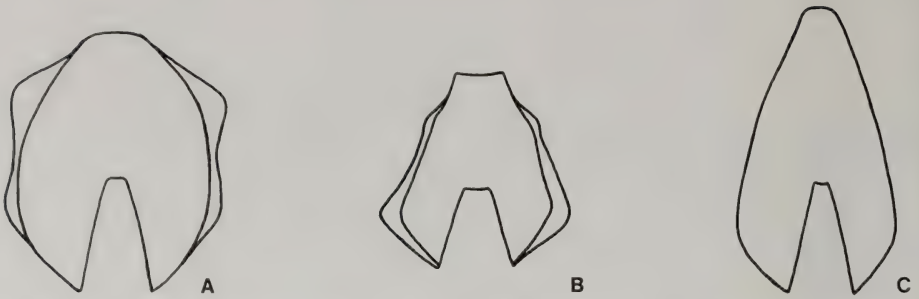


Fig. 39. *Placenticeraster kaffrarium* Etheridge, 1904. Whorl section of different specimens to illustrate variation. A. NMB D1150, '*kaffrarium*' type. B. NMB D1150, '*sub-kaffrarium*' type. C. NMB D1343, '*umkwelanense*' type.

(c) In some forms with smooth '*umkwelanense*' type ornament on the phragmocone, weak umbilica 1 only, or umbilical and lateral ornament, appears on the body chamber.

Dimorphism in the Zululand placenticeratids is restricted mainly to differences in size. In microconchs, which are more abundant in the present collection, the last septum is formed at diameters between 110 and 120 mm, whereas macroconchs show a wider range of maximum diameter, but generally form the last septum at between 150 and 185 mm. The length of the body chamber is between half and two-thirds of a whorl. Except for possibly one specimen, SAS Z1081 (Fig. 14A), no complete aperture was found and apertural modifications, if present, are unknown.

A combination of differing rates of ontogeny and dimorphism allows recognition of several morphotypes.

Type 1. In some specimens the shell never develops beyond the early smooth '*umkwelanense*' stage and remains smooth throughout. At the end of the adult phragmocone, and on the body chamber, however, the venter becomes distinctly rounded, albeit very narrow in extreme cases, without an intermediate tuberculate stage. There is considerable variation in the whorl section, ranging from extremely compressed, subtrigonal with flat flanks converging to a narrow venter, e.g. SAM-PCZ6197/a (macroconch) (Figs 40–41) to broadly rounded ovoid, e.g. SAM-PCZ6202 (macroconch) and NMB D1151/5 (microconch) (Figs 42–43) (also Figs 44–46B).

Type 2. In this form the greater part of the phragmocone remains smooth. Weak, poorly developed umbilical tubercles only start appearing on the late adult phragmocone or on the adult body chamber. Again, there is considerable variation in the whorl section, as in type 1. NMB D941/33 (macroconch) (Fig. 47) and SAS Z1065c (microconch) (Fig. 48) are good examples (also Figs 49–50).

Type 3. The greater part of the phragmocone is smooth, and ornament only starts appearing relatively late in ontogeny. On the adult body chamber, however,



Fig. 40. *Placenticerias kaffrarium* Etheridge, 1904. SAM-PCZ6197/a. Macroconch body chamber and last few septa of specimen with type 1 ornament. Note the extremely compressed, lanceolate whorl section and also the impression of the flat, entire venter of the inner 'umkwelanense' whorls. $\times 0,94$.



Fig. 41. *Placenticerias kaffrarium* Etheridge, 1904. SAM-PCZ6197/a. Macroconch body chamber and part of phragmocone with type 1 ornament. $\times 0,94$.



Fig. 42. *Placenticerias kaffrarium* Etheridge, 1904. NMB D1151/5. Microconch with type 1 ornament. Note the adult features—slight scaphitoid uncoiling, outward slanting of the umbilical wall and transition from flat to rounded venter. $\times 0,78$.



Fig. 43. *Placenticerus kaffrarium* Etheridge, 1904. NMB D1151/5. Microconch with type 1 ornament. $\times 0,78$.



Fig. 44. *Placenticeras kaffrarium* Etheridge, 1904. SAS Z1156. Macroconch with type 1 ornament. Note rounding of venter, outward-slanting umbilical wall and slight scaphitoid uncoiling towards beginning of body chamber. $\times 0,88$.



Fig. 45. *Placenticerus kaffrarium* Etheridge, 1904. SAS Z1156. Macroconch with type 1 ornament. $\times 0,88$.

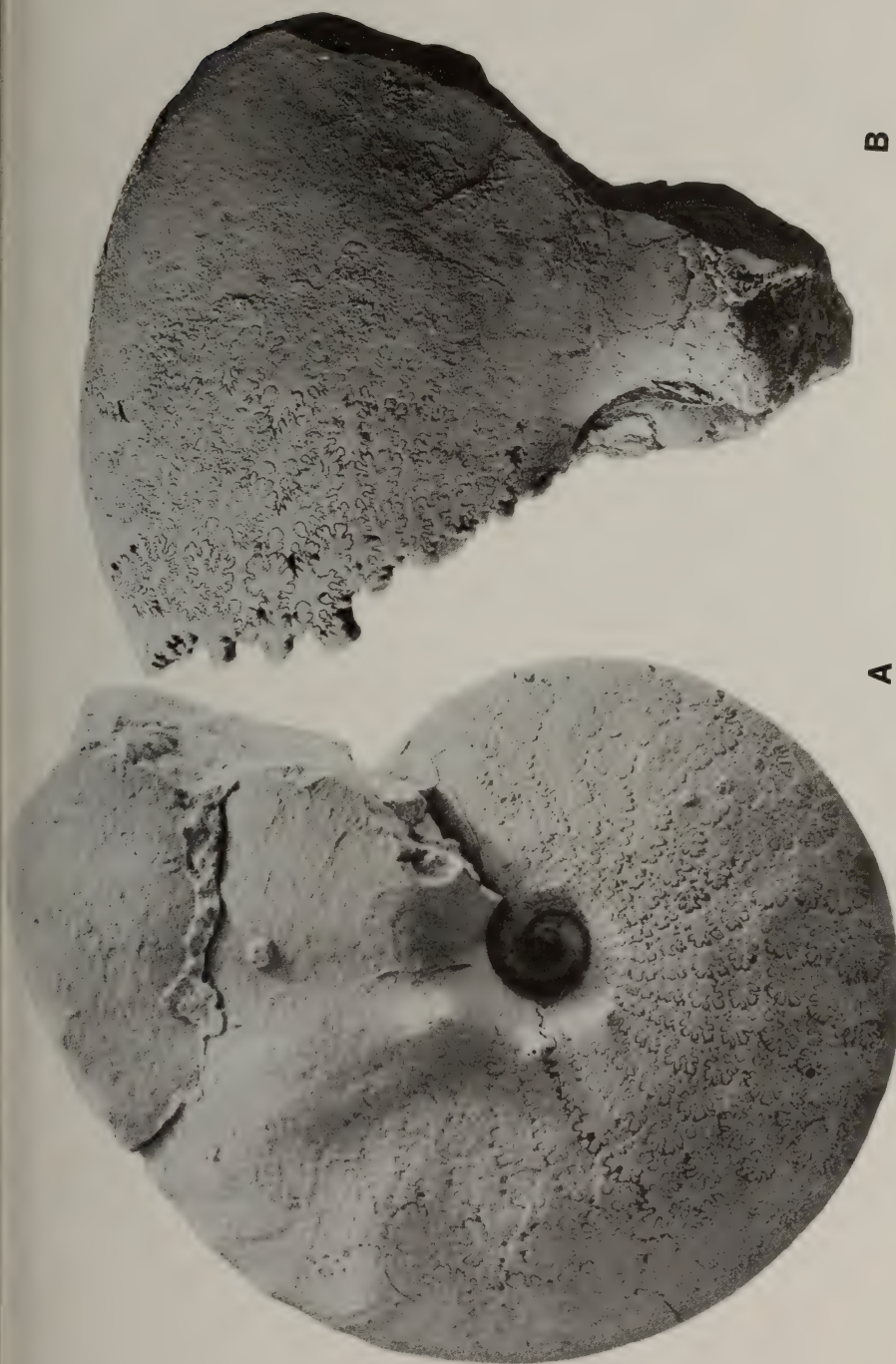


Fig. 46. *Placentiaceras kaffrarium* Etheridge, 1904. A. SAS Z680. Microconch with type 2 ornament in which umbilical tubercles only develop on the late phragmocone stage and on the body chamber. B. NMB D1343. Macroconch with type 1 ornament, retaining smooth 'umkwelanelense' stage up to the body chamber. Both $\times 1$.



Fig. 47. *Placenticeras kaffrarium* Etheridge, 1904. NMB D941/33. Macroconch with type 2 ornament in which umbilical tubercles only start appearing on the late phragmocone stage or on the body chamber. $\times 0,65$.



Fig. 48. *Placenticerias kaffrarium* Etheridge, 1904. SAS Z1065c. Microconch with type 2 ornament. $\times 0,88$.



Fig. 49. *Placenticerus kaffrarium* Etheridge, 1904. NMB D941/15. Microconch with type 2 ornament. $\times 1$.



Fig. 50. *Placenticerus kaffrarium* Etheridge, 1904. NMB D941/15. Microconch with type 2 ornament. $\times 1$.

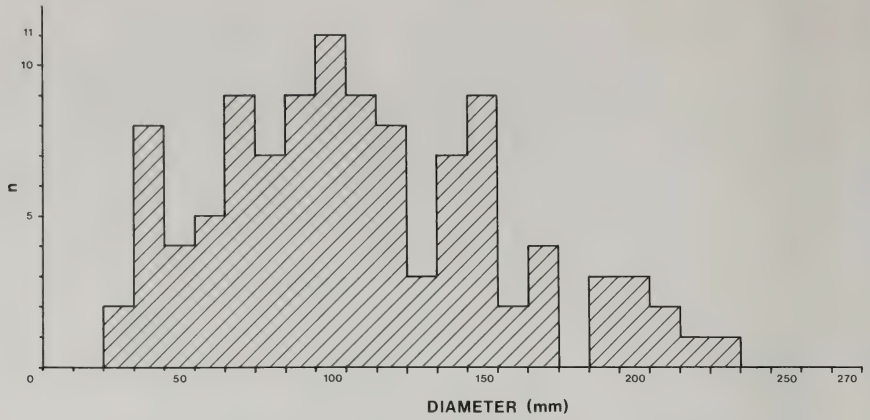


Fig. 51. *Placenticerus kaffrarium* Etheridge, 1904. Size distribution.

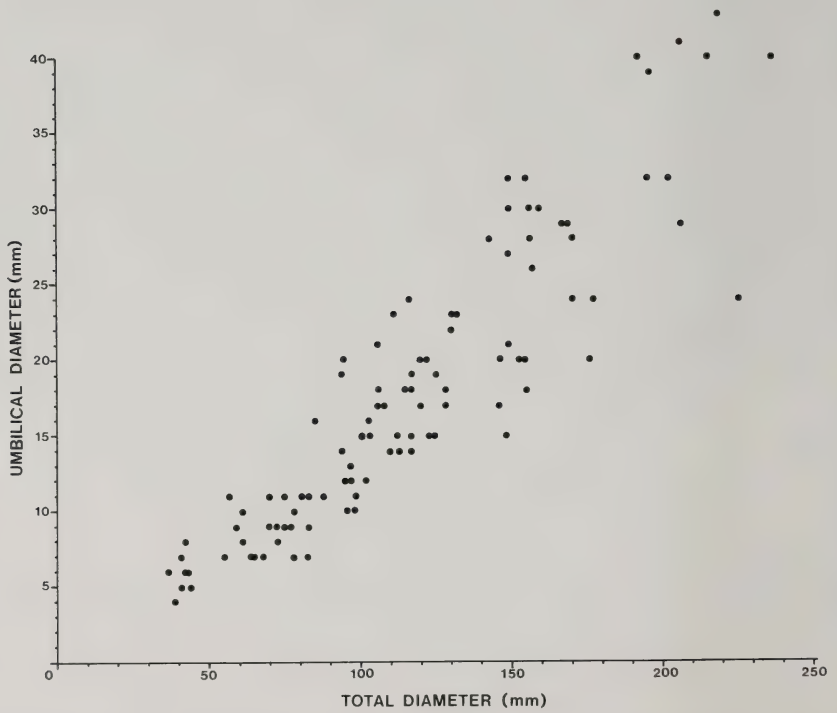


Fig. 52. *Placenticerus kaffrarium* Etheridge, 1904. Total diameter versus umbilical diameter.

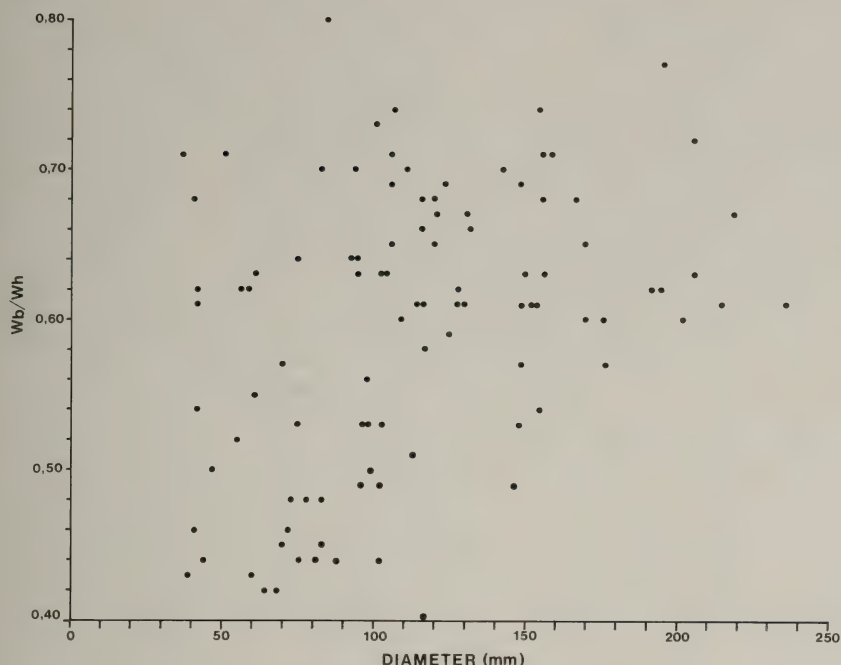


Fig. 53. *Placenticerias kaffrarium* Etheridge, 1904. Total diameter versus Wb/Wh.

ornament becomes quite bold, with distinct umbilical and lateral ornament of typical '*kaffrarium*' type. The venter changes from flat and smooth to tuberculate to rounded and smooth, or directly from flat and smooth to rounded and smooth without an intermediate tuberculate stage. Examples are SAS Z1520g (macroconch) and NMB D1269 (macroconch, Fig. 56).

These three morphotypes are all basically variations on the '*umkwelanense*' type of ornament, where the phragmocone remains predominantly smooth. In all the remaining groups, lateral ornament appears at a relatively early ontogenetic stage, and differences are found mainly in the relative strength of the umbilical and lateral ornament, and, in consequence, the whorl section.

Type 4. Here umbilical tubercles and ventral clavi develop at a very early stage, but no distinct lateral ribs or tubercles occur. The strength of the umbilical tubercles varies considerably, and in some cases they are markedly spinose. The umbilical tubercles generally weaken on the outer whorls and the flanks become rounded. Simultaneously, the ventral clavi may disappear and the venter may be flat and smooth as in '*umkwelanense*' morphotypes—especially on internal moulds—in association with weak umbilical tubercles, before becoming rounded.

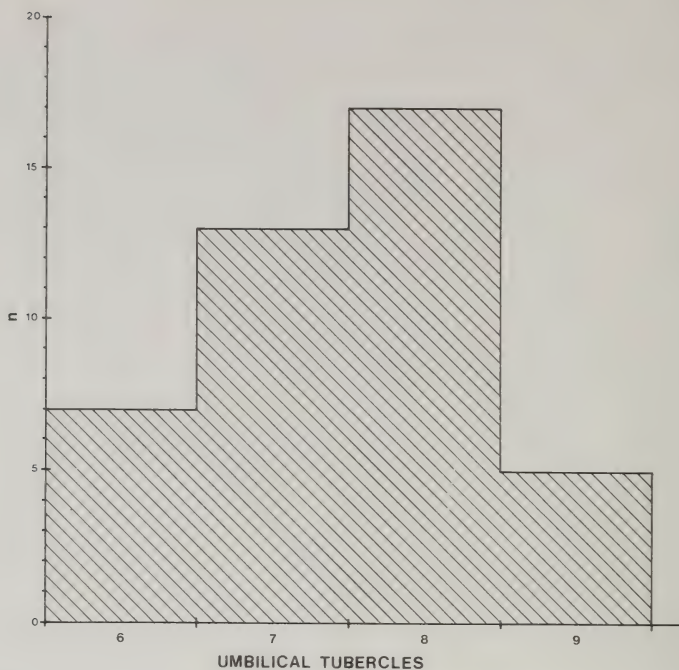


Fig. 54. *Placenticerus kaffrarium* Etheridge, 1904. Frequency of umbilical tubercles.

The whorl section is strongly subtrigonal with maximum whorl breadth at the site of the umbilical tubercle, but breadth to height ratios vary widely. This is the typical '*subkaffrarium*' type of sculpture where umbilical ornament is dominant, and the whorl section is distinctly subtrigonal. Typical examples are SAS Z201 (macroconch), SAS Z202 (macroconch) (Figs 57–58), NMB D941/2 (microconch) (Fig. 59), NMB D1267 (microconch) (Figs 60–61), SAM-PCZ6196 (microconch) (Figs 62–63), and NMB D925/3 (macroconch) (Figs 64–65) (see also Figs 66–68).

Type 5. Here the whorl section is still distinctly subtrigonal but, in addition to strong umbilical tubercles, strong lateral tubercles and strong ventral clavi occur, all connected by prominent ribs. On the adult outer whorls the section becomes rounded and ornament subdued. Examples are NMB D1271 (macroconch) (Fig. 69), SAS Z1520a (macroconch) (Fig. 72), NMB D941/19 (?macroconch) (Fig. 73); in some specimens, e.g. NMB D1269, D941/14 (Figs 70–71) fine, dense ribbing occurs on the outer adult whorls.

Type 6. In this type the lateral tubercle can become much stronger than the umbilical tubercle and the whorl section becomes polygonal at an early stage. In relation to the other types, ornament on the adult body chamber is strong but

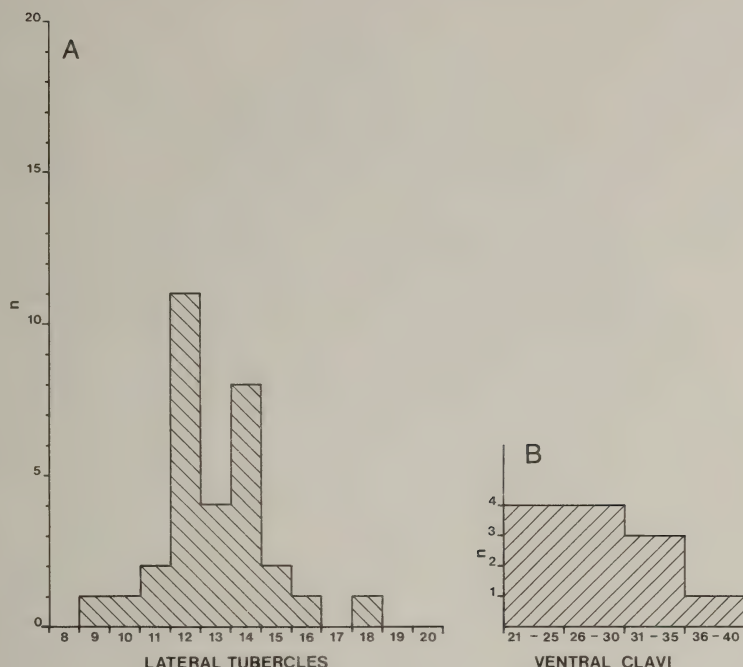


Fig. 55. *Placenticerus kaffrarium* Etheridge, 1904. A. Frequency of lateral tubercles. B. Frequency of ventral clavi.

nevertheless weaker than on the phragmocone. This is the typical '*kaffrarium*' type of ornament. Good examples are Z80 (microconch) (Figs 74–75), Z252 (macroconch) (Figs 76–77), Z1021 (macroconch) (Fig. 78), Z187 (microconch) (Fig. 79) (see also Figs 80–81).

Type 7. A few specimens, e.g. PCZ6215 (Fig. 82) show a very strong increase in ornament, passing rapidly from the smooth '*umkwelanense*' to very robust '*kaffrarium*' type of ornament (see also Figs 83–85).

3. Evolutionary changes

From the above description of the various morphological types encountered in Zululand Coniacian representatives of *Placenticerus*, it is clear that the material is extremely variable, and that we are dealing with but a single species.

Unfortunately no continuous exposures of the entire Coniacian Stage are available in Zululand. However, from the preliminary stratigraphic framework compiled by Kennedy & Klinger (1975), and partly revised for the Coniacian Stage by Klinger & Kennedy (1984), *Placenticerus* occurs in the lower three divisions of the Coniacian in Zululand, i.e. Coniacian I–III. In fact, *Placenticerus* already occurs in the basal *Pterotrigonia* conglomerate of the St Lucia Formation.



Fig. 56. *Placenticerias kaffrarium* Etheridge, 1904. NMB D1269. Part of body chamber of macroconch with type 3 ornament. $\times 1$.



Fig. 57. *Placenticerias kaffrarium* Etheridge, 1904. SAS Z202. Macroconch with type 4 ornament. $\times 0,72$.



Fig. 58. *Placentiaceras kaffrarium* Etheridge, 1904. SAS Z202. Macroconch with type 4 ornament. $\times 0,72$



Fig. 59. *Placenticeras kaffrarium* Etheridge, 1904. NMB D941/2. Microconch with type 4 ornament with umbilical spines weakening considerably on the outer whorls.



Fig. 60. *Placenticeras kaffrarium* Etheridge, 1904. NMB D1267. Microconch with type 4 ornament with umbilical tubercles and ventral clavi present at an early stage, but no lateral ornament. $\times 1,1$.

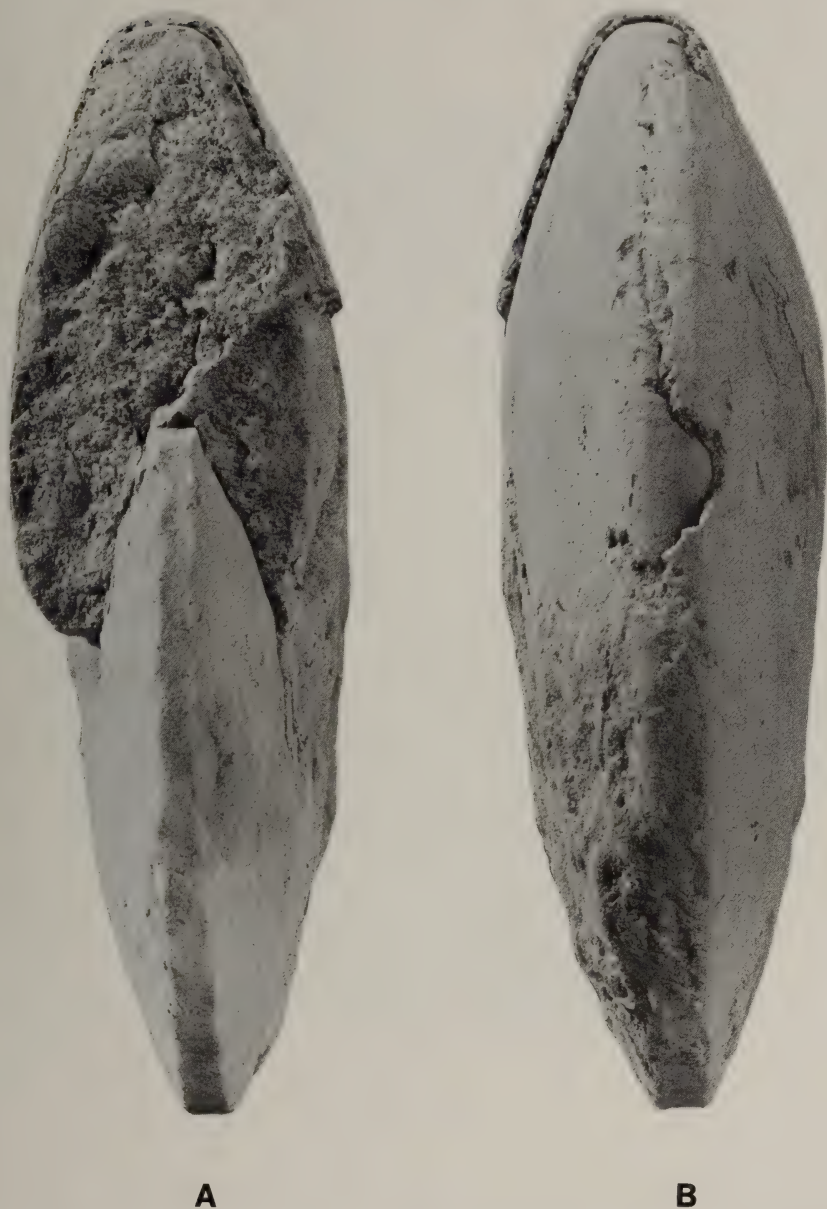


Fig. 61. *Placenticeras kaffrarium* Etheridge, 1904. NMB D1267. Microconch with type 4 ornament. $\times 1,1$.



Fig. 62. *Placenticerias kaffrarium* Etheridge, 1904. SAM-PCZ6196. Microconch with type 4 ornament.



Fig. 63. *Placenticerus kaffrarium* Etheridge, 1904. SAM-PCZ6196. Microconch with type 4 ornament.



Fig. 64. *Placenticerias kaffrarium* Etheridge, 1904. NMB D925/3. Macroconch with type 4 ornament. Note the decrease in strength of the umbilical tubercles towards the end of the phragmocone. $\times 0,85$.



Fig. 65. *Placenticerias kaffrarium* Etheridge, 1904. NMB D925/3. Macroconch with type 4 ornament. $\times 0,85$.



Fig. 66. *Placenticerus kaffrarium* Etheridge, 1904. NMB D1151. Macroconch with type 4 ornament. $\times 0,5$.



Fig. 67. *Placenticerus kaffrarium* Etheridge, 1904. SAM-PCZ6198. Impression of the inner whorl of specimens with type 4 ornamentation to illustrate spinose nature of umbilical tubercles and sigmoid lirae on the flanks. $\times 0,9$.



Fig. 68. *Placenticerus kaffrarium* Etheridge, 1904. SAM-PCZ6258. Impression of specimen with type 4 ornament to illustrate extremely spinose umbilical tubercles on inner whorls and fine lirae on flanks. $\times 0,8$.



Fig. 69. *Placenticeras kaffrarium* Etheridge, 1904. NMB D1271. Macroconch with type 5 ornament. $\times 0,75$.

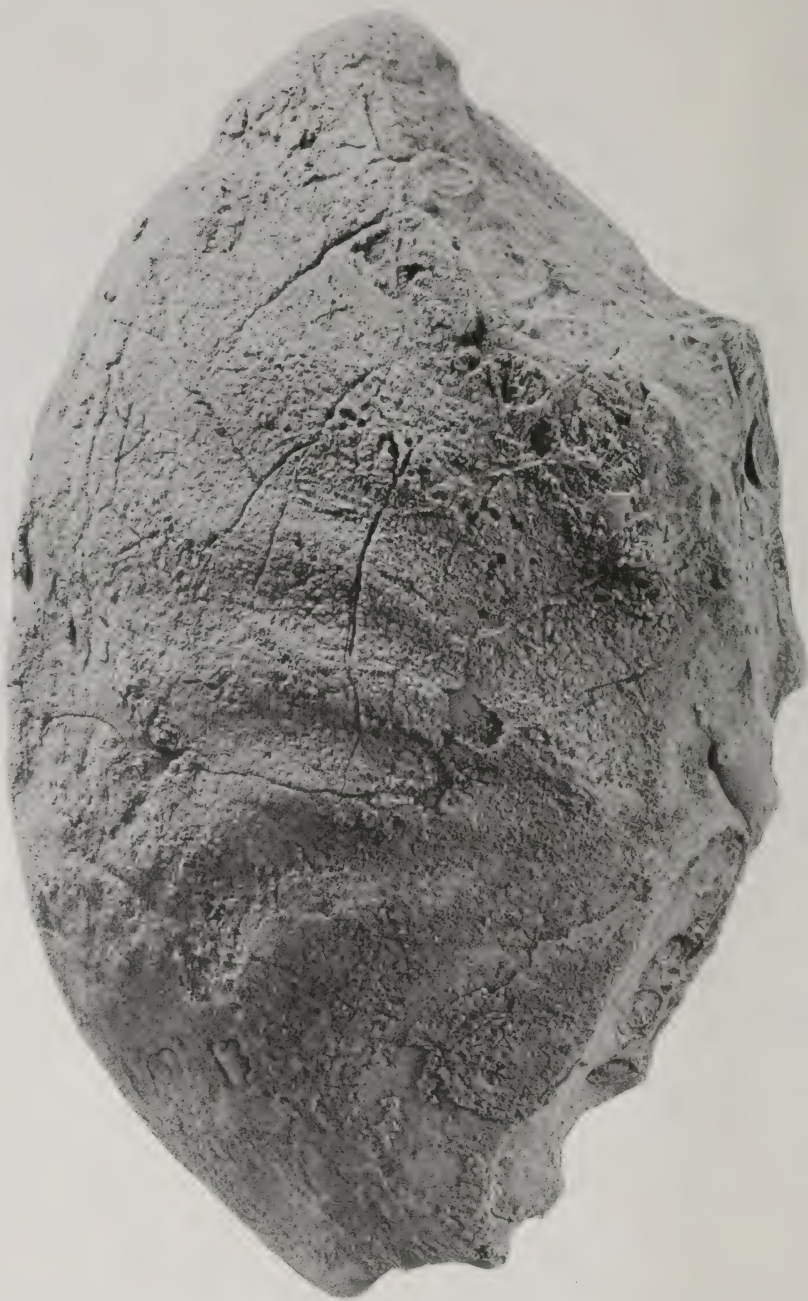


Fig. 70. *Placenticerus kaffrarium* Etheridge, 1904. NMB D941/14. Macroconch with type 5 ornament and fine, dense ribbing on the outer whorls. $\times 1$.



Fig. 71. *Placenticeras kaffrarium* Etheridge, 1904. NMB D941/14. Macroconch with type 5 ornament. Note the distinct 'subkaffrarium' inner whorls. $\times 1$.



Fig. 72. *Placenticerias kaffrarium* Etheridge, 1904. SAS Z1520a. Macroconch with type 5 ornament. $\times 0,75$.

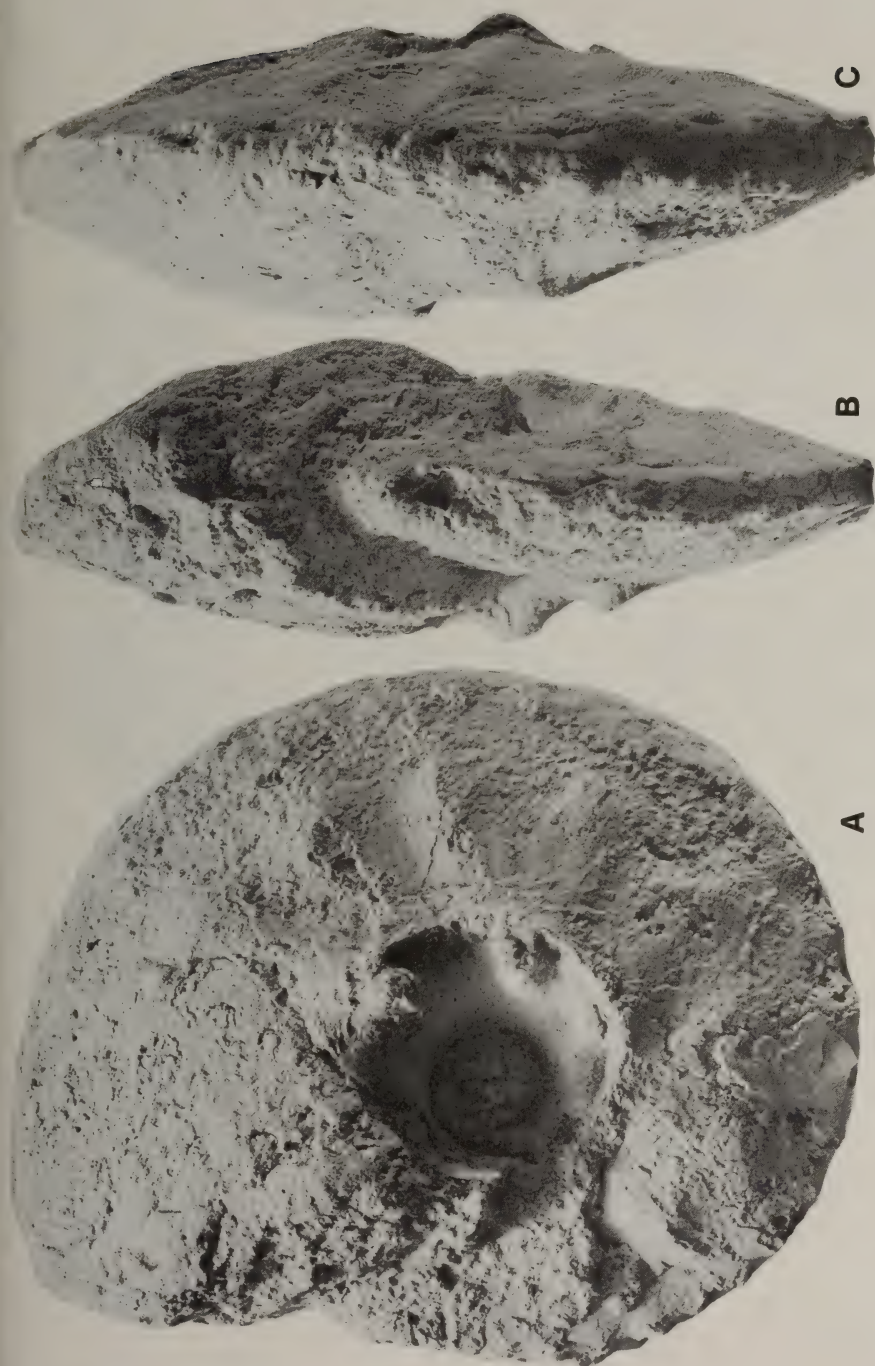


Fig. 73. *Placenticeras kaffrarium* Etheridge, 1904. NMB 941/19. Macroconch? with type 5 ornament. $\times 1$.



Fig. 74. *Placenticerias kaffrarium* Etheridge, 1904. SAS Z80. Microconch with type 6 ornament with strong lateral ornament at an early stage, resulting in distinct polygonal whorl section. $\times 1$.

**A****B**

Fig. 75. *Placenticerus kaffrarium* Etheridge, 1904. SAS Z80. Microconch with type 6 ornament with strong lateral ornament at an early stage, resulting in distinct polygonal whorl section. $\times 1$.



Fig. 76. *Placenticerus kaffrarium* Etheridge, 1904. SAS Z252/2. Macroconch with type 6 ornament. $\times 0,6$.



Fig. 77. *Placenticerias kaffrarium* Etheridge, 1904. SAS Z252/2. Macroconch with type 6 ornament. $\times 0,6$.

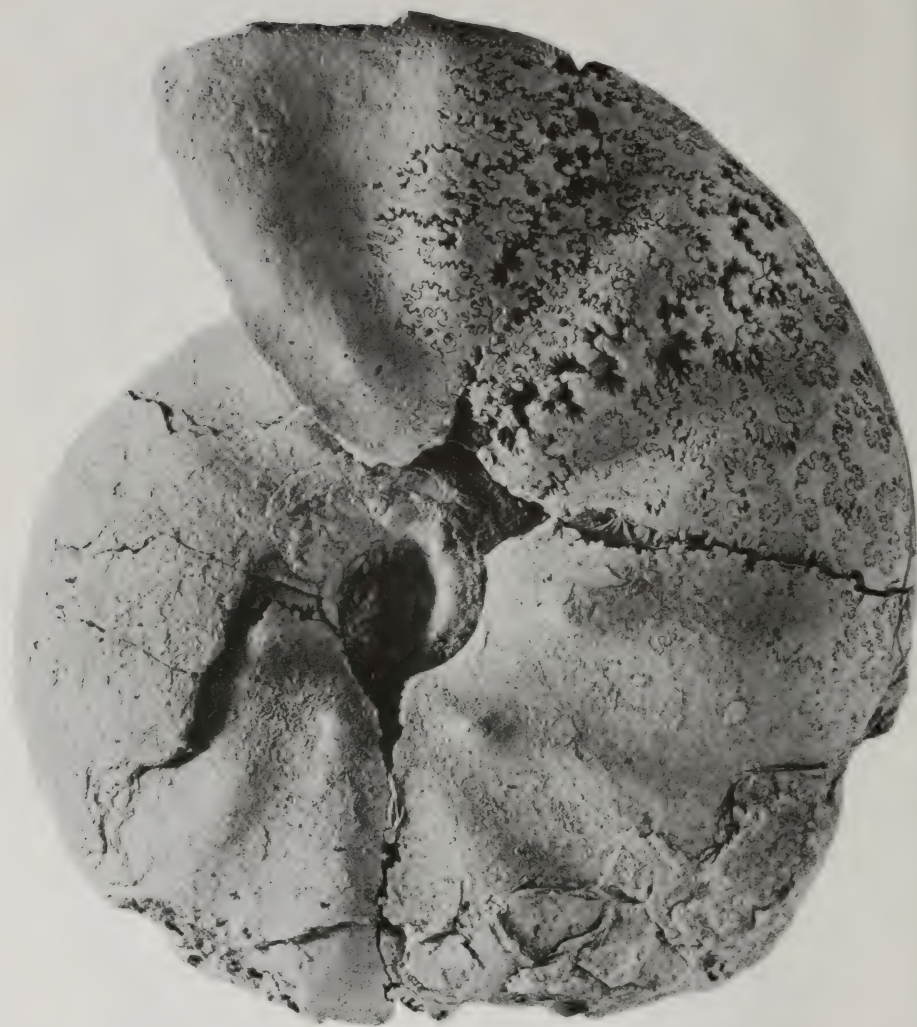


Fig. 78. *Placenticerus kaffrarium* Etheridge, 1904. SAS Z1021. Macroconch with type 6 ornament. $\times 0,7$.



Fig. 79. *Placenticerias kaffrarium* Etheridge, 1904. SAS Z187. Microconch with typical type 6 ornament. Note scaphitoid uncoiling of the body chamber. $\times 0,75$.



Fig. 80. *Placenticeras kaffrarium* Etheridge, 1904. SAS Z1125. Microconch with type 6 ornament. $\times 1$.



Fig. 81. *Placenticerias kaffrarium* Etheridge, 1904. NMB D1149/2. Microconch with type 6 ornament. $\times 0,80$.



Fig. 82. *Placenticerus kaffrarium* Etheridge, 1904. SAS Z215. Microconch with type 7 ornament. Note conical perforations on the bottom half of the shell. Possible signs of predation?
× 1.



Fig. 83. *Placenticerus kaffrarium* Etheridge, 1904. SAS Z890. Microconch with type 7 ornament with very strong, auricular lateral tubercles. $\times 1$.



Fig. 84. *Placenticerias kaffrarium* Etheridge, 1904. SAS Z1181. Microconch with type 7 ornament. $\times 1$.



Fig. 85. *Placenticerias kaffrarium* Etheridge, 1904. NMB D1150. Microconch with type 7 ornament. Note the strong lateral ornament and polygonal whorl section. $\times 1$.

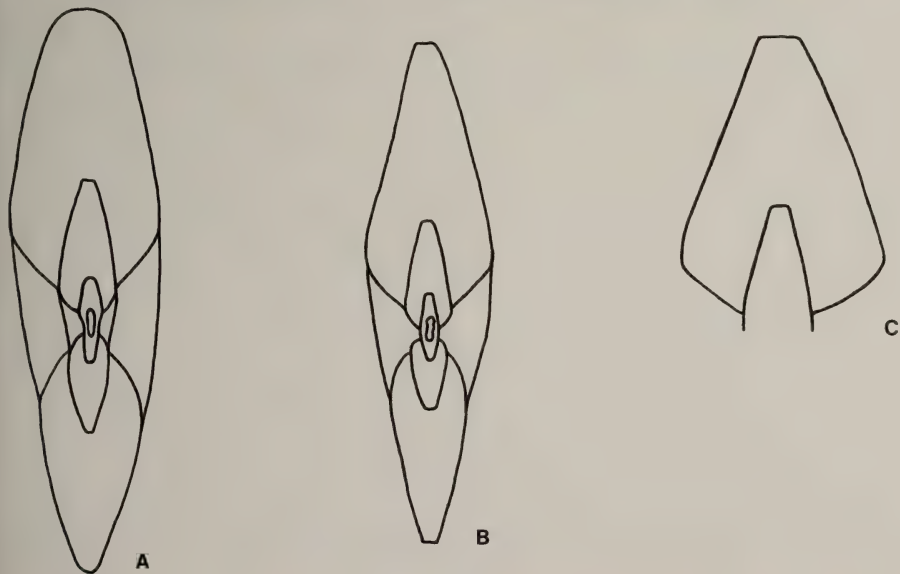


Fig. 86. *Placenticerias kaffrarium* Etheridge, 1904, uncatalogued. Whorl sections of three specimens, all from the same locality to illustrate variation in degree of inflation due to intraspecific variation. $\times 1$.



Fig. 87. *Placenticerus kaffrarium* Etheridge, 1904. Whorl section of extremely inflated specimen from the same locality as the specimens in Figure 86. $\times 1$.

overlying Upper Cenomanian sediments at locality 60 at the Skoenberg, Zululand (Fig. 20D). In the silts and sands overlying this basal conglomerate numerous representatives of *Placenticerus* occur. The '*umkwelanense*' and '*subkaffrarium*' forms are abundant, the latter being very obvious in the assemblage by virtue of the distinct subtrigonal whorl section and strong umbilical tuberculation. Forms with lateral ornamentation are also known but none approach typical *P. kaffrarium* forms. In the slightly younger *Placenticerus*-bearing strata (Coniacian II) along the lower reaches of the Mzinene River, at localities 71 and 72, and the lower reaches of the Hluhluwe River, at localities 92 and 93, '*umkwelanense*' and '*kaffrarium*' forms dominate. In the exposures along the Msundusi River at locality 145, the fauna seems similar to that of locality 60, but with elements of '*kaffrarium*' also present. This indicates that the Zululand *Placenticerus* are part

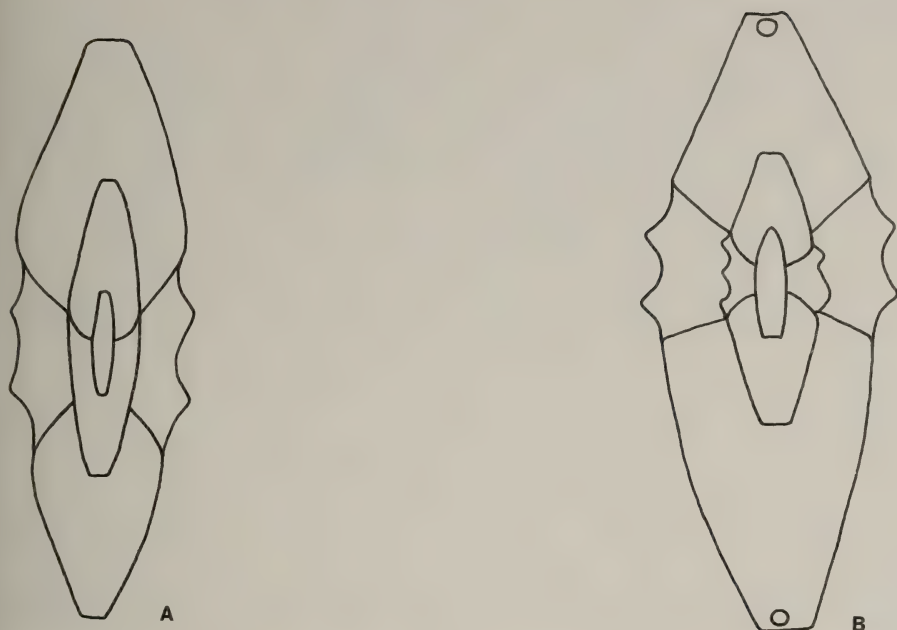


Fig. 88. *Placenticerias kaffrarium* Etheridge, 1904. Whorl sections of two specimens, both from the same locality as the specimens in Figures 86 and 87 to illustrate effects of intraspecific variation on whorl section. $\times 1$.

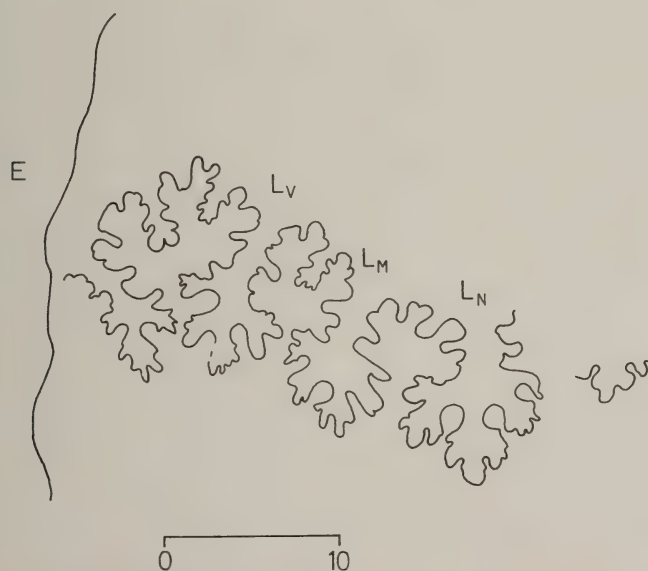


Fig. 89. *Placenticerias kaffrarium* Etheridge, 1904. SAS Z1442. Suture line of juvenile specimen. Scale bar in mm.

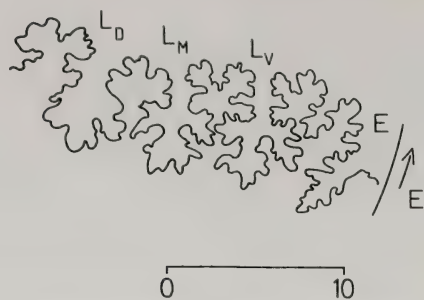


Fig. 90. *Placenticerus kaffrarium* Etheridge, 1904. SAS A1446. Suture line of juvenile specimen. Scale bar in mm.

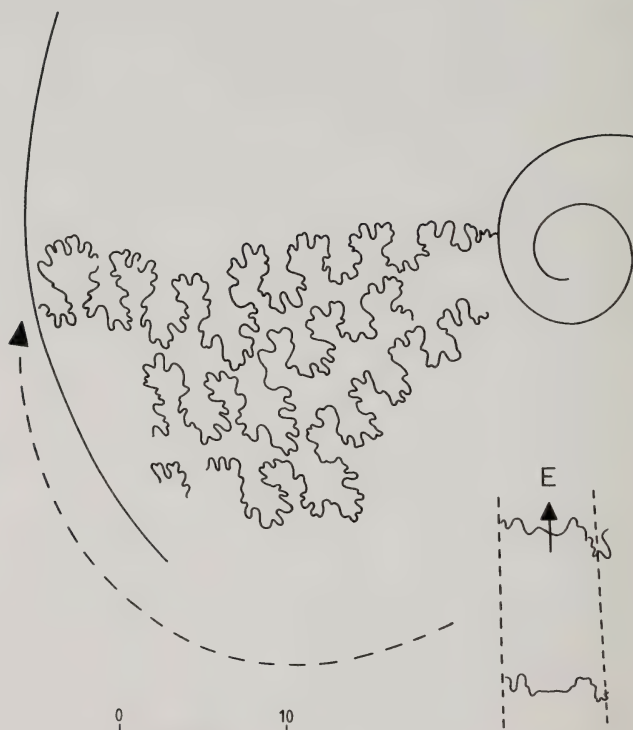


Fig. 91. *Placenticerus kaffrarium* Etheridge, 1904. Unregistered specimen. Suture line. Scale bar in mm.

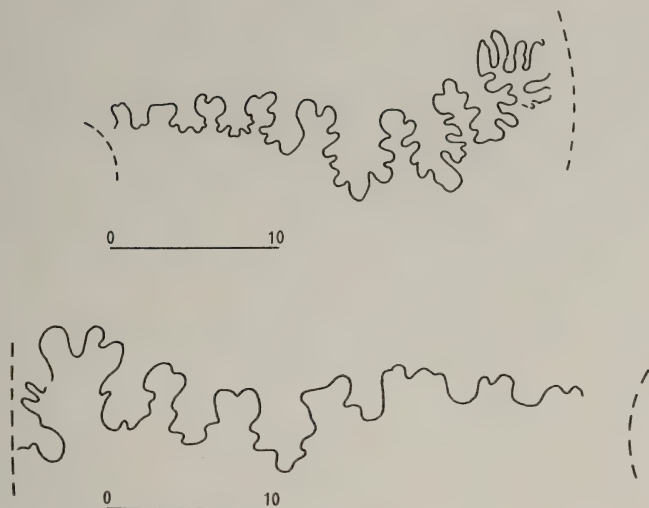


Fig. 92. *Placenticerias kaffrarium* Etheridge, 1904. Suture lines of SAS Z637 and NMB D941/4. Scale bar in mm.

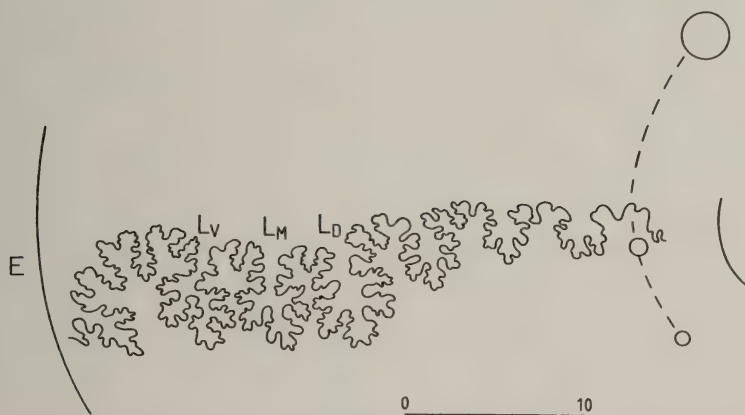


Fig. 93. *Placenticerias kaffrarium* Etheridge, 1904. SAS Z939. Suture line. Scale bar in mm.

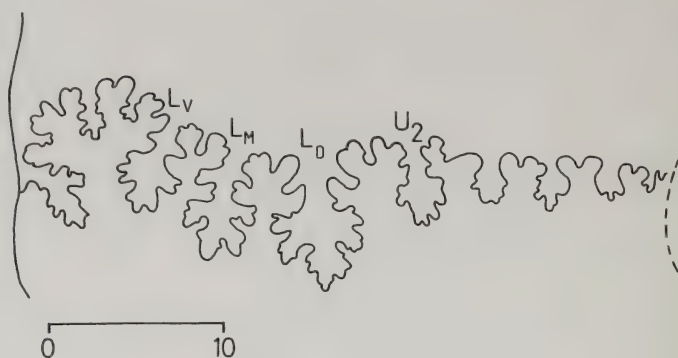


Fig. 94. *Placenticerias kaffrarium* Etheridge, 1904. Unregistered specimen. Suture line. Scale bar in mm.

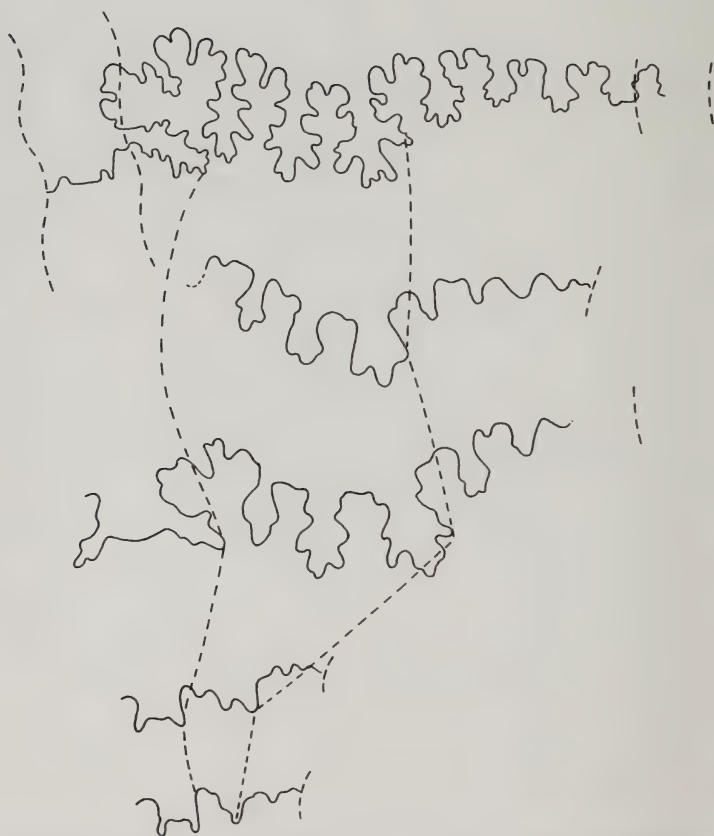


Fig. 95. *Placenticerias kaffrarium* Etheridge, 1904. Suture ontogeny. Unregistered specimen.

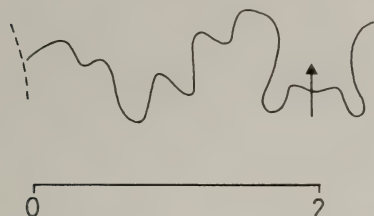


Fig. 96. *Placenticerias kaffrarium* Etheridge, 1904. NMB D941/7. Early suture. Scale bar in mm.

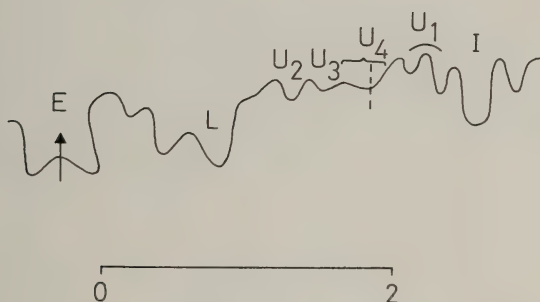


Fig. 97. *Placenticerias kaffrarium* Etheridge, 1904. NMB D941/7. Early suture. Scale bar in mm.

of a lineage in which early populations are dominated by '*subkaffrarium*' morphotypes with distinct trigonal whorl section and strong umbilical tubercles, succeeded by populations in which '*kaffrarium*' forms, with polygonal whorl section and lateral tubercles as strong or stronger than the umbilical ones dominate. At both levels feebly ornamented '*umkwelanense*' forms occur, retaining the smooth early stage to varying diameters.

At best, *subkaffrarium* and *kaffrarium* could be separated as chronological subspecies but given the presence of common morphotypes, even this is unnecessary, although given a number of specimens it is possible to distinguish early and late forms of the species. More important, the Zululand material shows unequivocal evidence of progressive evolutionary change in a single lineage: phyletic gradualism.

4. Intraspecific variation

Intraspecific variation *per se* is difficult to separate completely from the other variable factors affecting differences in placenticeratid populations. Obvious variation is reflected by reference to various morphotypes, but here differing rates

of ontogenetic development and, to a lesser degree, phylogenetic changes are also involved. True intraspecific variation is best seen in different degrees of inflation of the whorl section. A number of specimens from the same restricted stratigraphic level (Figs 86–88) show the total spectrum of intraspecific variation in this character—ranging from a compressed, flat-sided whorl section to an inflated, trigonal whorl section with greatest width at the umbilical shoulder.

Unfortunately the material is not suitable for studying detailed sutural ontogeny. Available sutures are shown in Figures 89–97 to show the variation.

Discussion

From the above description it is clear that all the *Placenticer* from the Coniacian of Zululand belong to a single extremely variable but phylogenetically conservative species, for which we select the name *Placenticer kaffrarium*. This had already been suggested on earlier occasions (Klinger & Kennedy 1980b, 1980c), and is now confirmed. All the other names used for Zululand *Placenticer*, i.e. *P. umkwelanense* Etheridge, 1904, *P. subkaffrarium* Spath, 1921, *P. cf. subkaffrarium* Spath, 1921, *Placenticer* n. sp. aff. *kaffrarium* Venzo, 1936, merely represent different ontogenetic stages or intraspecific variants of *P. kaffrarium*.

In view of the intraspecific variation, comparisons with material from other regions are difficult. This is painfully obvious in the works of Boule *et al.* (1907), Besairié (1930) and Venzo (1936); all identified feebly ornamented, Coniacian, ‘*umkwelanense*’ morphotypes with the smooth Campanian species *Placenticer whitfieldi*.

Forms similar to *P. kaffrarium* have been recorded from the Middle and Upper Turonian of Madagascar under the names *Proplacenticer memoriae-schloenbachi* Laube & Bruder var. *ambiloensis* Collignon (1965a: 14, 16, pl. 381 (fig. 1646), pl. 382 (figs 1647–1648)), *Parastantonoceras murphyi* Collignon (1965a: 17, pl. 382 (fig. 1649)), *Proplacenticer stantoni* Hyatt var. *fortior* Collignon (1965a: 19, pl. 383 (fig. 1652)) and *Proplacenticer orbignyi* (Geinitz) (Collignon 1965a: 20, pl. 383 (figs 1653–1654)). Nearly all these ‘species’ and varieties can be matched in the material from the Coniacian of Zululand and we regard them as synonyms, although the structure of Turonian *Placenticer* populations in this area remains unknown.

The Coniacian stratigraphy of Madagascar has recently been reviewed by the authors (Klinger & Kennedy 1984), clarifying Collignon’s (1965b) usage of the terms Lower, Middle and Upper Coniacian. Collignon’s Lower and Middle Coniacian zones of *Peroniceras dravidicum* and *P. subtricarinatum*, and of *Kossmaticeras theobaldi* and *Barroisiceras onilahyense*, correspond approximately to the second and third divisions of the Coniacian stage in Zululand, and the Middle Coniacian of France, as defined by the authors.

Proplacenticer aff. *fritschii* de Grossouvre var. *eboroensis* Collignon (1965b: 38, pl. 430 (figs 1780–1781)) from Collignon’s Middle Coniacian corresponds to the typical *Placenticer kaffrarium* (Type 2), with umbilical tubercles appearing

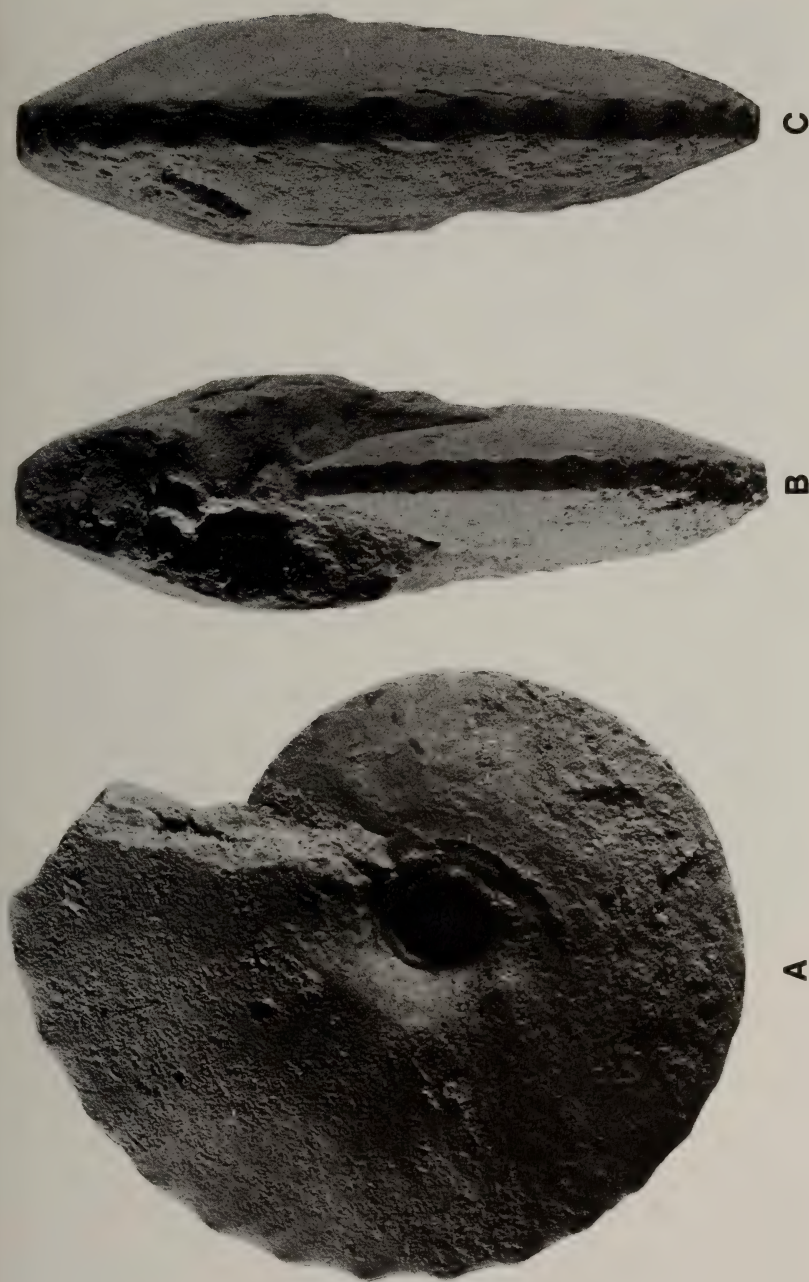


Fig. 98. *Placenticerus kaffrarium* Etheridge, 1904, SAM-6523. The holotype of *Placenticerus reinecke* Haughton, 1925, from Angola. $\times 1$.



Fig. 99. *Placenticerias* ?*kaffrarium* Etheridge, 1904. The holotype of *Placenticerias merenskyi* Haughton, 1930, from the Wanderfeld IV Beds near Bogenfels, South West Africa–Namibia.

× 1.

at a relatively late stage. Specimens such as Z680 from Zululand match this variety perfectly.

Proplacenticerias sp. nov. (Venzo) aff. *kaffrarium* Etheridge (Collignon 1965b: 40, pl. 431 (fig. 1783)) appears to be a microconch of *P. kaffrarium* with subdued outer flank ornament. *Proplacenticerias satriense* Collignon (1965b: 40, pl. 431 (fig. 1782)) closely matches Zululand *P. kaffrarium* (Type 4) macroconchs such as SAS Z202. Both these forms were recorded from the Upper Coniacian of Madagascar, i.e. Middle Coniacian *sensu* Klinger & Kennedy 1983.



Fig. 100. *Placenticerus ?kaffrarium* Etheridge, 1904. Holotype of *Placenticerus merenskyi* Haughton, 1930, SAM-10569, from the Wanderfeld IV Beds near Bogenfels, South West Africa-Namibia. $\times 1$.

Comparisons with material from further afield than Madagascar are difficult and must be viewed with some caution—especially as we do not have detailed descriptions of large populations. The effects of geographic isolation and perhaps geographic subspecies development may merit valid taxonomic separation of these forms.



Fig. 101. *Placenticerus fritschi* de Grossouvre, 1894. Cast of the lectotype (EMP collections); the original of De Grossouvre (1894, pl. 5 (fig. 1)) from the Calcaires Durs de la Ribochère of La Ribochère (Loir-et-Cher) France. $\times 1$.

The following named species belong to the group of *Placenticerus kaffrarium*:
Placenticerus reinecke Haughton (1925: 271, pl. 13 (figs 4–5)) (also 1926: 15, pl. 2 (figs 4–5)—French translation) (Fig. 98). Holotype by monotypy SAM-6523 from south of the river Massango, Angola. In addition to the holotype we have studied 10 specimens from San Nicolau, Angola (ex M. R. Cooper collection). These specimens show the same range of ontogenetic and intraspecific variation as *P. kaffrarium*. Haughton's view that this species differs from *P. subkaffrarium*



Fig. 102. *Placenticerus fritschi* de Grossouvre, 1894. Cast of the lectotype (EMP collections); the original of De Grossouvre (1894, pl. 5 (fig. 1)) from the Calcaires Durs de la Ribochère of La Ribochère (Loir-et-Cher) France. $\times 1$.

in having a smaller whorl breadth and greater number of ventral clavi is not supported by the study of the additional material now available. The San Nicolau locality was dated as Turonian–Lower Coniacian by Cooper (1978).

Placenticerus merenskyi Haughton (1930: 363, pl. 11 (figs 1–3)) (see also Klinger 1977, fig. 7) (Figs 99–100). Holotype, by monotypy SAM-10569 from the Cretaceous (Cenomanian?) of Bogenfels, Namibia (see also McLachlan & McMillan 1979). This is a difficult species to interpret, being based on a single specimen in



Fig. 103. *Placenticerias fritschi* de Grossouvre, 1894. FSR unregistered specimen from the Calcaires Durs de la Ribochère of La Ribochère (Loir-et-Cher) France. $\times 1$.

poor preservation. The flanks appear to be smooth and the venter flat and entire. The umbilicus is partially occluded by matrix and encrusting ostreids but, although probably wider than in most *P. kaffrarium*, is nevertheless within the limits of the species. Umbilical ornament consists of about 12 small, pinched tubercles, which is more than the average 7–8 in *P. kaffrarium*. Also, the presence of umbilical tubercles in *P. kaffrarium* is normally associated with a tuberculate venter. This places it closer to the Turonian material from Madagascar described by Collignon (1965a) as *Proplacenticerias memoriaschloenbachi* var. *ambiloensis* which, according to present interpretation, corresponds to type 2 or 4 of *P. kaffrarium*.

Placenticerias memoriaschloenbachi Laube & Bruder (1887: 221, pl. 23 (fig. 1)). Quite what this species actually is, remains problematic. The original highly schematic figures show it to have 10 spirally elongated, umbilical tubercles, and a narrow venter with sharp shoulders and no ventral clavi to a great diameter. This



Fig. 104. *Placenticerias fritschi* de Grossouvre, 1894. SP unregistered specimen from Saujon, La Pompière (Charente-Maritime), France. $\times 1$.

species is known from the Cenomanian to Turonian of west and Central Europe. The combination of umbilical tubercles with a narrow, smooth, non-tuberculate venter seem sufficient at present to separate it from the mainstream of *P. kaffrarium*.

Placenticerias fritschi de Grossouvre (1894: 124, pl. 5 (figs 1–2), text-fig. 52) (Figs 101–104) was recently reviewed by Kennedy (1984). The lectotype of the species is the larger specimen figured by De Grossouvre (pl. 5 (fig. 1)). This species has about ten small umbilical tubercles from an early stage, and twice as



Fig. 105. *Placenticerus semiornatum* (d'Orbigny, 1850). A-B. Paralectotype. C-D. Lectotype. Both from Touraine, France; horizon uncertain, but probably Santonian. $\times 1$.



Fig. 106. *Placenticerus semiornatus* (d'Orbigny, 1850). MNHP 1986-27 from the Craie de Villedieu of St Fraimbault (Sarthe) France. $\times 1$.

many crescentic lateral ribs and an entire venter—apparently never developing ventral clavi. Again, the combination of umbilical tubercles with non-tuberculate venter may serve as a basis for separation from mainstream *P. kaffrarium*. Its relationship to *P. memoriaschloenbachi* remains uncertain.

Placenticerus kharesmense Lahusen (1884: 134, pl. 2, pl. 3 (fig. 1)) (see also Archanguelski 1916: 40, pl. 6 (fig. 5), pl. 7 (fig. 1)), originally described from the Turonian of Turkestan, is similar to forms of *P. kaffrarium* with umbilical tubercles only—i.e. 'subkaffrarium', and given more material may prove to be conspecific, the name having priority over *P. kaffrarium*.

Placenticerus kysylcumense Archanguelski (1916: 45, pl. 7 (figs 4-7)) has an inflated whorl section, strong umbilical and lateral tubercles and ventral clavi. This is very difficult to distinguish from robust forms of *P. kaffrarium* and may be conspecific. Kennedy (1984) suggested that it may be the microconch of *P. kharesmense*.

Placenticerus semiornatus (d'Orbigny, 1850), also recently reviewed by Kennedy (1984) (Figs 105–106), can generally be distinguished from *P. kaffrarium* by virtue of the absence of umbilical tubercles throughout (as far as can be ascertained from the poor type material); it does, however, bear strong resemblance to smooth 'umkwelanense'.

Beschtubeites beschtubensis Iljin (1975: 163, pl. 29 (figs 1–2), pl. 34 (fig. 7)) from the Lower Turonian of the Amur River is a finely ornamented placenticeratid, and may be distinguished from *P. kaffrarium* by virtue of the greater number of lateral tubercles per whorl and ribs per whorl (25–29).

Beschtubeites kutuzovae Iljin (1975: 164, pl. 29 (fig. 3), pl. 34 (fig. 8)) is another slightly coarser ribbed form with about 20–24 lateral tubercles per whorl.

Proplacenticerus kotzi Iljin (1975: 165, pl. 30 (figs 1–2), pl. 34 (fig. 9)), from the Lower Coniacian of Central Asia, is similar to the forms of *P. kaffrarium* that retain the smooth 'umkwelanense' stage up to the body chamber without crenulation of the venter and only there develop a few feeble tubercles.

Proplacenticerus proplanum Iljin (1975: 166, pl. 31 (fig. 2), pl. 35 (fig. 10)), from the Upper Coniacian of Central Asia, has 4–5 small umbilical tubercles and a smooth venter, thus resembling *Placenticerus fritschi* de Grossouvre.

Indian material

Proplacenticerus rampuraensis Chiplonkar & Ghare (1977a: 109, figs 1–2, 6A, D) and *Proplacenticerus spathi* Chiplonkar & Ghare (1977a: 110, fig. 7E–F), from the Turonian Nodular Limestone at Rampura, also appear to be typical *P. kaffrarium*. *Proplacenticerus fritschi* (de Grossouvre) of Chiplonkar & Ghare (1977a: 113, fig. 7B–C), from the Turonian Limestone at Bagh, Mahakal, Rampura, etc., is poorly preserved, but probably also belongs to *P. kaffrarium*.

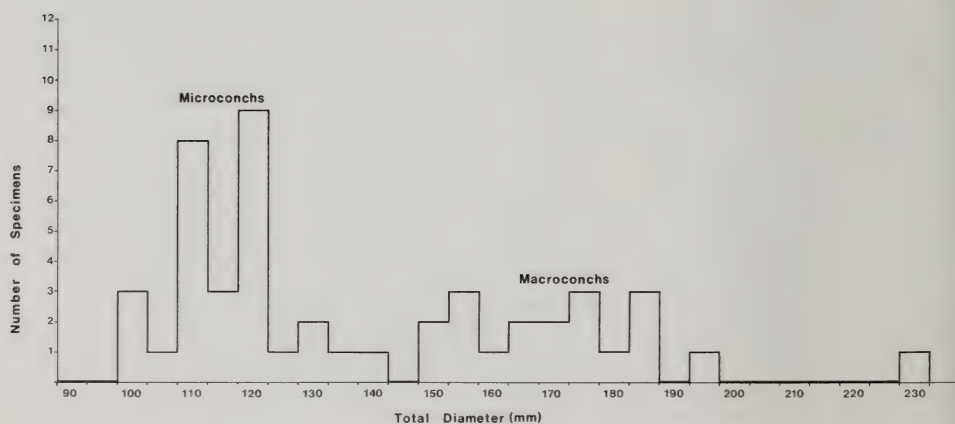


Fig. 107. Histogram indicating frequency distribution of macroconchs and microconchs in *Placenticerus kaffrarium* Etheridge, 1904.

Proplacenticerias stantoni (Hyatt, 1903) Chiplonkar & Ghare (1977a: 114), from the Turonian Nodular Limestone, north of Bagh Caves, Rampura and Mahakal, was not figured and we cannot comment on it. *Pseudoplacenticerias* sp. cf. *P. milleri* (von Hauer, 1866) (Chiplonkar & Ghare 1977a: 115, fig. 6E–F) is from the Turonian purple shales between Nimar Sandstone and Nodular Limestone at Bagh caves. This differs from mainstream *P. kaffrarium* in only having feeble ventral clavi and no lateral ornament.

All the specimens from the Narmada Valley Basin described by Chiplonkar & Ghare (1977b) as *Placentoscaphites* are no more than adult placenticeratids, some possibly deformed by compaction, with scaphitoid uncoiling of the body chamber. *Placentoscaphites helicus* Chiplonkar & Ghare (1977b: 74, pl. 2 (figs 3–4)) with helical inner whorls seems to be either pathological or secondarily deformed.

Occurrence

Turonian and Coniacian of Madagascar, Coniacian I–III of Zululand, Alphard Group offshore Cape Province, Turonian of India?, questionably Wanderfeld IV beds of Namibia, and 'Turonian–Coniacian' of Angola.

Genus *Hoplitoplacenticerias* Paulcke, 1907

Type species: Hoplites plasticus plasticus Paulcke, 1907 (p. 186) (ICZN opinion 554, 1959; name no. 1629).

Discussion

In the most recent review of the Placenticeratidae, Kennedy & Wright (1983: 868) stated quite emphatically that 'Two stocks (which) separated from *Placenticerias* in the Santonian . . . (*Hoplitoplacenticerias* and *Metaplacenticerias*) . . . clearly deserve generic separation'. However, analysis of the type material of German *Hoplitoplacenticerias* and Zululand material, as well as a review of the literature, indicate that the intraspecific variation in these two groups is as great as that found in normal *Placenticerias*, which not only clouds differences between the two genera (*Hoplitoplacenticerias* and *Metaplacenticerias*) but also from the mainstream *Placenticerias*.

Both genera were originally poorly defined. The combination *Hoplites Placenticerias* was used by Paulcke (1907) in his description of an Upper Cretaceous fauna from Cerro Cazador in southern Patagonia. According to Paulcke this fauna could be traced back to Lower Cretaceous hoplitid ancestors but, on the other hand, showed features that constituted transitions to *Placenticerias*. On examining the fauna, Paulcke faced the question of where to place it—in *Hoplites* or in *Placenticerias*—or whether to erect a new genus. Paulcke favoured transitional genera, which exhibited features of both ancestral and descendant genera. He suggested that, rather than to erect a meaningless new name ('bei denen sich kein Mensch etwas denken kann'), both names should be

used to indicate, from the nomenclature, from where and in which direction development took place; that part of the morphology which was dominant in the material should be emphasized ('hervorheben'). If hoplitid features dominated the name should be *Hoplitoplacenticeras*, whereas, if placenticeratid features dominate, the name would be *Placenticeras*. Transitional forms between *Hoplites* and *Placenticeras* would be designated *Hoplitoplacenticeras*. If neither was dominant, neither part of the name would be italicized. This procedure was contrary to the rules and the name *Hoplitoplacenticeras* was validated in 1959 in ICZN opinion 554.

Wright (1957: L392) defined *Hoplitoplacenticeras* as 'Rather evolute for family; whorl section compressed to trapezoidal, venter flat; with prominent variable coarse rounded or dense fine ribs, nearly straight, bearing 2 rows of ventrolateral tubercles, of which outer row may be large and clavate; ribs cross venter transversely and may have trace of siphonal tubercle. Genus is probably too widely drawn'. Kennedy & Wright (1983: 870) repeated this diagnosis almost word for word.

Kennedy (1986) provided a very detailed discussion of *Hoplitoplacenticeras*, based on examination of Schlüter's (1867, 1871–1876) type material from Northern Germany. Apart from expanding on the generic diagnosis originally provided by Wright (1957) and Kennedy & Wright (1983), Kennedy also stabilized *Hoplitoplacenticeras* nomenclature by designating lectotypes for the German species. Schlüter referred the same specimens to different names on the three occasions he discussed the group, and subsequent authors made type designations that were ambiguous or invalid.

Examination of North German and Zululand material by both of us shows that *Hoplitoplacenticeras* is as variable during the Upper Campanian to Upper Maastrichtian as is *Placenticeras* during the Cenomanian to Maastrichtian.

As far as the shape of the whorl section is concerned (compressed or inflated), the variation in *Hoplitoplacenticeras* matches that of *Placenticeras*—compare e.g. *H. costulosum* (Schlüter, 1867) with *H. dolbergense* (Schlüter, 1876). Ornament is as variable, ranging from virtually smooth in *H. costulosum*, save for fine sigmoid striae and poorly developed umbilical tubercles, through moderately ornate *H. marroti* (Coquand, 1859) with trituberculate ribbing, to strongly ornamented *H. dolbergense* (Schlüter). The umbilical tubercles may remain at the umbilical edge as in *H. vari* or *H. costulosum*. In *H. lemfoerdense* an additional row of ventral tubercles develops. *H. lemfoerdense* thus has a set of mid-lateral, inner and outer ventrolateral and ventral tubercles. This peculiar arrangement of tubercles is also shown by the Upper Maastrichtian *H. lafresnay-anum* (d'Orbigny, 1841), recently revised by Kennedy (1986). For this distinctive group Kennedy (1986) has proposed the subgenus *H. (Lemfoerdiceras)*, type species *H. lemfoerdense* (Schlüter, 1872).

The only apparent difference between *Placenticeras* and *Hoplitoplacenticeras*, as far as ornament is concerned, seems to be the positioning of the external clavi. In *Placenticeras* they always alternate on either side of the venter, whereas

in *Hoplitoplacenticeras* they correspond in all species except *H. coesfeldiense schlueteri* Michailov, 1951. (But Cobban (pers. comm.) says there are American specimens of *P. intercalare* that have matched clavi and alternate clavi on the same individual.) As far as this feature is concerned, *Placenticeras polyopsis* appears transitional to *Hoplitoplacenticeras* in the adult stage—the position of the clavi changing from alternating to only slightly offset. Another apparent difference seems to be that a smooth *Placenticeras* juvenile stage has never been found in *Hoplitoplacenticeras*. Also, as far as we know, fine, thread-like ribbing has never been observed in adult *Placenticeras*.

According to the diagnosis given by Wright (1957), there may be traces of a siphonal row of tubercles. The only species with distinct siphonal tubercles are *Hoplitoplacenticeras awadi* (Hassan 1971: 71, pl. 2 (figs 8–9)) and *H. kambysis* (Quaas 1902: 309, pl. 29 (figs 8–11)) from the Maastrichtian of Egypt. The latter species is in fact a scaphitid, according to Dr Z. Lewy (pers. comm. 1985). Kennedy (1986) regarded both as scaphitine homoeomorphs of *Hoplitoplacenticeras*.

As far as the suture lines are concerned, we have to rely mainly on the work of Paulcke (1907). Fortunately the Patagonian material allowed him to examine the sutures in detail through all stages of growth. What is of interest here is that the sutures change according to ontogeny and morphology.

The sutures of Patagonian *Hoplitoplacenticeras* are not in the least pseudoceratitic, neither in the juvenile nor in the adult stage (Fig. 110). They are ammonitic throughout. In the juvenile stage the lateral lobe (L) is distinctly trifid; the saddle E/L is broad and from a very early stage already shows a prominent incision. The adult sutures vary considerably and, according to Paulcke, the variation is largely determined by the whorl section and ornament. In those forms with inflated whorl section and strong ornament, e.g. *H. p. hauthali* Paulcke, the lateral lobe remains more or less symmetrically trifid and independent, and the first lateral saddle (E/L) entire. In forms where placenticeratid features dominate, i.e., typically compressed whorl section and involute coiling, e.g. *H. p. laevis* Paulcke, the lateral lobe becomes remarkably asymmetrical until the ventral prong of the lobe is almost as long as the median one, thus giving the lobe a nearly bifid appearance, and the incision in the first lateral saddle (E/L) becomes very prominent and nearly as deep as the prongs of the lateral lobe. Also, the saddles and lobes tend to become constricted near their bases.

To summarize, *Hoplitoplacenticeras* can be distinguished from *Placenticeras* mainly by virtue of the ventral tubercles corresponding and an apparent lack of a smooth juvenile stage.

Distinction between *Hoplitoplacenticeras* and *Metaplacenticeras* in terms of the type species is easy. *Metaplacenticeras* was introduced by Spath (1926: 79) in cryptic manner '*Metaplacenticeras* gen. nov., proposed for *Placenticeras pacificum* J. P. Smith ("Development and Phylogeny of *Placenticeras*". . .) This last is characterized by its falcoid ribbing and has a suture-line distinct from that of the typical *Placenticeras placenta* (DeKay).'

The most comprehensive discussion on *Metaplacenticer* was given by Reeside (1926). As far as ornament is concerned, the type species has a tricarinate venter to a diameter of 100 mm; in the adult stage the venter is narrow and flat or slightly concave, bordered by finely nodose keels.

According to Reeside's interpretation of the genus, it included species such as *Placenticer* *californicum* Anderson, *P. sanctaemonicae* Waring 'and probably also some of the forms included by Paulcke under the names *Hoplites plasticus-costatus* and *H. plasticus-laevis*, from the Senonian of Patagonia' (Reeside 1926: 2). Apart from the central keel, which may, in some cases, be only be weakly developed, allocation of species such as *Placenticer* *californicum* to either genus seems feasible. Both genera have overlapping stratigraphic ranges in the Upper Campanian in Japan (Matsumoto 1982a, 1982b), but in North America *Hoplitoplacenticer* seems to occur slightly earlier than *Metaplacenticer*. For the present it seems advisable to retain the two genera, though fully aware of the range of overlap.

Matsumoto (1984: 20–21) recently discussed the genus *Metaplacenticer* and alleged that a true adventive lobe (A) was present in the suture. This is totally at variance with views held by Schindewolf (see above, p. 263). In addition, Matsumoto doubted if both *Metaplacenticer* and *Hoplitoplacenticer* belonged to Placenticeratidae—tentatively suggesting a pseudoschloenbachid origin for *Hoplitoplacenticer*.

Occurrence

Hoplitoplacenticer occurs world-wide in the Upper Campanian, and ranges to the Upper Maastrichtian in western Europe. It has been reported from Germany (Schlüter 1867, 1872–1876; Giers 1964; Schmid & Ernst 1975), France (De Grossouvre 1894), European Russia (Michailov 1951), Central Asia (Atabekian & Khakhimov 1976), Don basin (Naidin 1974), Poland (Nowak 1909), Sweden (Ødum 1953), Spain (Basse 1931), Israel (Chavan 1947), Libya (Maxia 1943), Madagascar (Basse 1931; Collignon 1970), Egypt (Mahmoud 1955), Angola (Howarth 1965; SAM collections), Zululand (Kennedy & Klinger 1975), Natal (Kennedy & Klinger 1973), Patagonia (Paulcke 1907), Wyoming (Cobban 1963), Texas (Young 1963), British Columbia (Usher 1952; Ward 1978), and Japan (Matsumoto 1982a, 1982b, 1984).

Hoplitoplacenticer *howarthi* Collignon, 1970

Figs 108–109

Hoplitoplacenticer *howarthi* Collignon, 1970: 80, pl. 639 (fig. 2351).

Hoplitoplacenticer *plasticum plasticum* Paulcke: Kennedy & Klinger, 1973: 102, pl. 5 (fig. 4a–e).

Type

Holotype, by original designation, the original of Collignon (1970: 80, pl. 639 (fig. 2351)) from the Upper Campanian of Mokotibe (Antsalova), Madagascar.

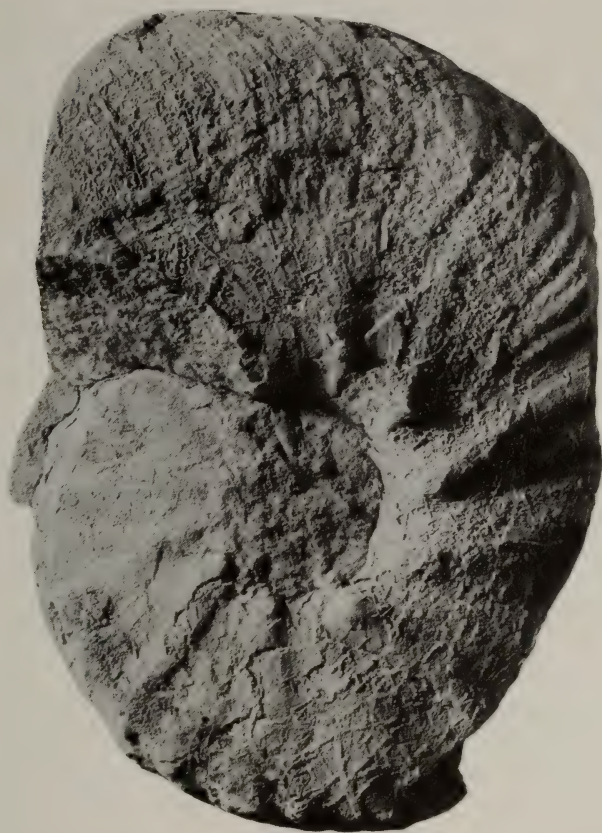


Fig. 108. *Hoplitoplacenticeras howarthi* Collignon, 1970. SAM-PCZ6586. Macroconch. $\times 1$.

Material

SAS Z646, NMB D1314, SAM-PCZ6586–6587, all from locality 110, cliff and foreshore section at the south-western tip of the Nibela Peninsula, St Lucia Formation, Campanian III. University of Natal specimens 6556, from Somtseu Road, Durban.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>	<i>Ut</i>	<i>Vt</i>
PCZ6586	107	39 (36,4)	49 (45,8)	0,79	22 (20,6)	11	—
D1314	70	—	29 (41,4)	—	20 (28,6)	8	—

Description

The available specimens show virtually all the stages of ornamentation except those of the early embryonic stage. On the inner whorls of Z646 (Fig. 109) the



Fig. 109. *Hoplitoplacenticeras howarthi* Collignon, 1970. SAS Z646. Microconch. $\times 1$.

very early, poorly developed *Placenticeras*-like ornament can be seen, soon to be followed by the very coarse ornament of the greater part of the phragmocone. This consists of low, single and bifurcating ribs. They arise on the umbilical wall, giving rise to obliquely elongated tubercles from which they either bifurcate or cross the flanks undivided. The ribs are rather low and sinuous on the flanks and some show incipient looping. Near the ventrolateral shoulder they give rise to a ventrolateral clavus, curve slightly forward and end in outer ventral clavi. The ventrolateral and ventral clavi correspond on either side of the venter. This type of ornament is present in all four specimens, but that of D1314 (Fig. 14B) is most prominent with near horn-like ventrolateral tubercles on the outer whorl. PCZ6586 (Fig. 108) shows the adult ornament of the body chamber. Here the prominent lateral and ventral ornament of the phragmocone is replaced by fine, thread-like lirae, and the venter becomes more or less rounded. Part of the suture is exposed in PCZ6587.

Discussion

The Zululand material closely matches the Madagascan holotype at the same diameter. Given the wide variation in placenticeratids, we doubt that the seven other species described from the same locality by Collignon are anything more than intraspecific variants of a single species.

The small specimen from the subsurface deposits of Durban originally described as *H. plasticum plasticum* (Kennedy & Klinger 1973: 102, pl. 5 (figs 4a-e)) matches the Zululand material and is best referred to *H. howarthi*.

Occurrence

Upper Campanian of Zululand, Natal and Madagascar.

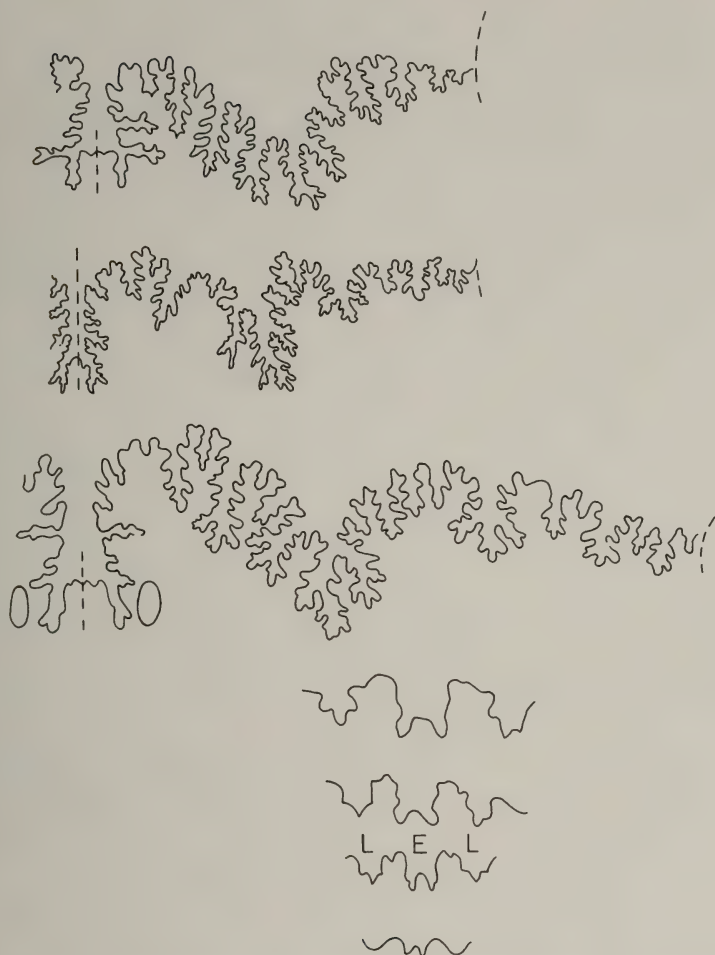


Fig. 110. Suture ontogeny of *Hoplitoplacenticeras*. Composite drawing. (After Paulcke 1907, text-figs 10a, 5, 10b-c, 8, 12, 25, bottom to top.)

THE SYSTEMATIC POSITION OF THE GENUS *HYPENGONOCERAS*

Genus *Hypengonoceras* Spath, 1922

Type species. *Placenticeras warthi* Kossmat (1895: 176, pl. 20 (fig. 8)) (= *Ammonites Orbignyanus* Stoliczka (*non* Geinitz) (1864: 92, pl. 48 (fig. 2)) from the Lower Utatur Group (Albian) of southern India, by the original designation of Spath (1922: 112).

Diagnosis

Narrowly umbilicate, shell compressed; flanks generally little rounded. Ornament consists of low falcoid ribs, often very weak and only visible under oblique lighting. Umbilical tubercles may be present but are never very prominent. Venter flat to concave, with alternating ventral clavi at least at some stage. Dimorphism pronounced, but mainly restricted to differences in size. Macroconchs may reach diameters up to half a metre; microconchs up to 100 mm. Suture variable; in typical forms some saddles are little divided and 'pincer-like' with bifid folioles; in others as incised as in normal placenticeratid pattern.

Discussion

The genus *Hypengonoceras* was introduced in characteristically brief style by Spath (1922: 112) as follows: 'The Engonoceratidae include *Hypengonoceras*, nov., proposed for the Albian "*Placenticer*" (type: *Pl. warthi*, Kossmat, "Untersuch. üb. d. Südind. Kreidef.," loc. cit., 1895 p. 80, pl. xx, fig. 8; and STOLICZKA, loc. cit., p. 92, pl. xlviii, fig. 2) = group IV of *Placenticer* in VREDENBURG ("Amm. of the Bagh Beds," Rec. Geol. Surv. India, vol. xxxvi, pt. 2, 1907, p. 120). They are clearly derivatives of *Hoplitida*, and have no direct relationship either with the Mammitid *Placenticer* or with *Hoplitoplacenticer* (so-called "*Hoplites*") of the Senonian.'

Correct interpretation of the genus, as well as its systematic position, is disputed.

In terms of Vredenburg's (1907) original diagnosis of his 'Section IV' (of *Placenticer*), for which Spath created the genus *Hypengonoceras*, only the type species belongs here. This section is 'Compressed; smooth, outermost subsidiary saddle split into two portions by a deep adventitious lobe, so that the external saddle appears divided into four portions instead of three; the suture has numerous inflections, but is very slightly frilled, the summit of the saddles being almost devoid of marginals with the exception of a deep narrow median notch' (Vredenburg 1907: 119).

Adkins (1928: 260) referred *Hypengonoceras* to the family Engonoceratidae, but Spath later (1931: 340) referred the genus to the Placenticeratidae without stating any reasons. Roman (1938: 869) put the genus in the family Placenticeratidae.

Casey (1960: 208) stated of *Hypengonoceras* 'With its simple, pincer-like endings to the saddles, *Hypengonoceras* shows great resemblance to the Engonoceratids *Knemiceras* and *Parengonoceras* of Lower and Middle Albian age, though it exhibits the more complex fragmentation of external saddle characteristic of the Placenticeratidae . . . nothing is known, however, to bridge the gap between *Hypengonoceras* and the rather diverse forms that comprise the Upper Cretaceous Placenticeratidae. . . . It is probable that both *Hypengonoceras* and *Hengestites* are forerunners rather than direct ancestors of the Upper Cretaceous Placenticeratidae.' Even Schindewolf (1967: 744) casually referred *Hypengono-*

ceras to the Placenticeratidae in suggesting that the sutural ontogeny of the genus probably is similar to that of *Metaplacenticerias*.

Kossmat's (1895: 170 (74)) observation that *A. warthi* differs from the other placenticeratids in that the external saddle is subdivided into four instead of three auxiliary saddles which slope gently down to the first lateral lobe seems to have received little subsequent attention.

Up to that stage, *Hypengonoceras* was interpreted in terms of the type species *H. warthi*, known from the Upper Albian of southern India (Stoliczka 1865; Kossmat 1895) and possibly Madagascar (Boule *et al.* 1907) only, and the diagnosis provided by Vredenburg (1907), Wright (1957) and Casey (1960) regarding the pincer-like saddles and generally simple suture sufficed. However, since then, several other species have been referred to *Hypengonoceras* that blur the apparent simple image of the genus. *Hypengonoceras decaryi* Collignon (1963: 128, pl. 291 (fig. 1269)) is known from the Upper Albian, Zone of *Pervinquieria inflata* of Madagascar, and was also recorded from Mozambique by Förster (1975: 216, pl. 10 (fig. 7), text-fig. 64) and is now known from Zululand (see below). This is a very large species; the diameter of the wholly septate holotype is 240 mm. Ornament consists of low, rib-like swellings, and, according to Förster, 8 to 10 prorsiradiate umbilical bullae per whorl. It retains the clavate venter to a very large diameter, before eventually becoming smooth. What is noteworthy, is that the saddles in the suture line are by no means as pincer-like as in the type species (Fig. 17). In fact, were it not known that the species occurs in the Albian, it could be regarded as a normal '*Proplacenticerias*'. Collignon (1963: 126, pl. 290 (fig. 1268)) in fact described another species from the same locality and stratigraphic level (Mont Raynaud, Diego-Suarez) as *Proplacenticerias rerati*. The species is based on a similarly large holotype, still septate at 240 mm diameter, with low ribbing originating from weak, conical umbilical tubercles. The venter also shows the same transition from tuberculate with long clavi to smooth. The suture is very little incised. Apart from differences in umbilical diameter and ornament between the two species, they are well within the range of intraspecific variation in placenticeratids. They are probably conspecific or at least congeneric.

Three more species were described by Collignon (1966) from the Upper Albian Zone of *Dipoloceras cristatum* of Tarfaya. *Hypengonoceras chouberti* Collignon (1966: 17, pl. 4 (figs 1-1a, 2-2a), pl. 5 (fig. 127)) is another enormous species. The largest fragment figured by Collignon (1966, pl. 5) has a whorl height of 137 mm. The inner whorls of the species are coarsely ornamented, but it becomes smooth on the outer whorls. *Hypengonoceras fauremuretae* Collignon (1966: 18, pl. 6 (fig. 1-1a, 2-2a, 3-3a, 4-4a)) is virtually smooth throughout as compared to *H. chouberti* and has well-developed ventral carinae with tiny clavi. The sutures, however, especially the lobes are typically rounded and splayed like the 'fingers of a glove'. *Hypengonoceras tarfayense* Collignon (1966: 19, pl. 7 (fig. 1-1a)) is another gigantic species with measured maximum diameter (still septate) of 236 mm. It has delicate ventral clavi which eventually disappear on the phragmocone, resulting in a smooth, rounded venter. Lateral ornament consists

of fine, dense costules only. The suture line is poorly preserved, but seems to have rather massive rectangular saddles and narrow lobes.

Arias & Wiedmann (1977: 9, fig. 5) described *Hypengonoceras ibericum* from the Albian Utrillas Beds of south-eastern Spain. This is very strongly ornamented form with 10 prorsiradiate to sinusoidal ribs, each originating at a small umbilical tubercle, bearing a lateral tubercle and ending in a ventrolateral tubercle, at which point they bifurcate, and eventually terminate in external clavi on the venter. Quadrituberculate ornament is hitherto unknown in *Hypengonoceras*—and we doubt if *H. ibericum* is in fact correctly referred to *Hypengonoceras*, and suggest it is probably a *Knemiceras*. *Hypengonoceras ibericum* apart, *Hypengonoceras* is now no longer as simple to interpret as initially conceived.

Two questions have to be answered: Is *Hypengonoceras* a member of the Engonoceratidae or of the Placenticeratidae? If the latter, what is its relationship with the early placenticeratids '*Karamaites*' and *Hengestites*?

Engonoceratidae and Placenticeratidae are generally distinguished by the simplified, ceratitic saddles of Engonoceratidae, as compared to finely incised saddles and lobes of Placenticeratidae. As far as this criterion is concerned *Hypengonoceras* is transitional between Engonoceratidae and Placenticeratidae—but then so is *Parengonoceras* Spath, 1924, which has always unquestionably been regarded as a member of the Engonoceratidae. Schindewolf (1967: 745) has argued that a reduction of a placenticeratid suture to that of an engonoceratid is possible, but that the reverse (if *Hypengonoceras* were to be referred to Placenticeratidae) is less likely, though possible. Thus, as far as the general outline of the saddles is concerned, *Hypengonoceras* could be referred to either family, though the majority of known specimens would seem better placed in Engonoceratidae.

As far as details of the suture line are concerned, the first significant (and up to now only) attempt at trying to establish the systematic position of *Hypengonoceras*, was by Renz (1970: 1028) in an introduction to the genus *Parengonoceras*. Freely translated Renz stated that 'The suture lines seem to be of significant importance in distinguishing between *Parengonoceras* and *Hypengonoceras*. Reference is made to two illustrations of external sutures: the one of the holotype, and a second of a fragment from the Cenomanian of Mont Raynaud in Madagascar (Boule *et al.* 1907, text-fig. 26, p. 46). The external saddle is characteristic, in being clearly narrower than in *Parengonoceras*, and is divided into two halves by a deep incision, which could correspond to a third adventive lobe. The question of whether we are here dealing with real adventive lobes or only with subdivisions (Teilprodukte) of the lateral lobe, will be significant for allocation of this group to Engonoceratidae or Placenticeratidae.' The importance of seeking real grounds for separating *Hypengonoceras* from *Parengonoceras* becomes even more obvious in Renz's (1970) description of the Andean representatives of *Parengonoceras*. *Parengonoceras discoides* Renz, 1970, is described as being externally similar to *Hypengonoceras fauremuretae* Collignon, 1963 (Renz 1970: 1036); *Parengonoceras barbacoense* Renz, 1970, was initially (Renz

1968: 626) identified as a *Hypengonoceras*, and later (1970: 1044) compared with *Hypengonoceras warthi* as far as the narrow bifid saddles are concerned, and with *Hypengonoceras decaryi* Collignon and *H. fauremuretae* Collignon as far as the lack of ornament.

Despite the (superficial?) similarity between *Parengonoceras* and *Hypengonoceras*, there was never any doubt about the systematic placing of the former genus. Again we suspect that this systematic grouping had been influenced more by stratigraphy than natural affinities. Being of Lower to Middle Albian age, *Parengonoceras* was more naturally placed in the predominantly Lower Cretaceous Engonoceratidae, rather than the predominantly Upper Cretaceous Placenticeratidae. As far as the sutural ontogeny is concerned, there is little doubt that *Parengonoceras* has two true adventive lobes, and that the lateral lobe remains simple (Fig. 18). The lateral lobe (L) and the adjacent adventive lobe (A_1) are nearly equal in size, and slightly deeper than the flanking U_2 and A_2 lobes, giving the ventral part of the external suture a bow-like sagging appearance, quite unlike the typical sagging zig-zag outline of typical Placenticeratidae. In addition, the lobes are splayed and digitate—like the fingers of a glove. No detailed ontogenetic studies have as yet been undertaken on *Hypengonoceras*, neither is the available material from Zululand suitably preserved for such studies. As far as the general outline of the external suture of *H. warthi* is concerned, however, apart from the width of the lateral saddle, it shows far greater similarity to *Parengonoceras* than to *Placenticeratidae*. Also, the relative proportions of the umbilical lobes, U_2 and U_3 ('fourth and fifth lateral lobes') is similar to that of later (Turonian and younger) '*Proplacenticeratidae*' rather than that of early '*Karamaites*'. Thus on these grounds, *Hypengonoceras* can be clearly ruled out from the direct line of ancestry of *Placenticeratidae*. Casey (1960: 208) had already suggested that *Hypengonoceras* and *Hengestites* be regarded as forerunners, rather than direct ancestors of the Upper Cretaceous Placenticeratidae. Casey (1960: 208), however, reiterated the accepted view of *Hypengonoceras* bearing strong resemblance to Engonoceratidae, and considered derivation of *Hypengonoceras* from *Parengonoceras* or some allied member of the Engonoceratidae probable. Recent data (e.g. Mirzoev 1967; Michailova 1974, 1978) have unequivocally shown the origin of early *Placenticeratidae* ('*Karamaites*') to lie in the Hoplitidae, and not in the Engonoceratidae. These data would then suggest that *Hypengonoceras* would be better treated as a late Upper Albian member of the Engonoceratidae, rather than as an early placenticeratid of unknown affinities, as tentatively suggested in Kennedy & Wright's (1983, text-fig. 5) phylogenetic diagram.

Occurrence

Albian of India (Stoliczka 1863–1865; Kossmat 1895), Madagascar (Collignon 1963; Boule *et al.* 1907), Mozambique (Förster 1975), Zululand (Kennedy & Klinger 1975), Israel (Lewy 1981), Morocco (Collignon 1966), and Saghalin (Matsumoto 1942).

Hypengonoceras decaryi Collignon, 1963

Figs 111–126

Placenticeras Warthi Boule, Lemoine & Thévenin, 1907 [*non* Kossmat]: 26 (46), pl. 12 (5) (fig. 6–6a).

Hypengonoceras decaryi Collignon, 1963: 128, pl. 291 (fig. 1269). Förster, 1975: 216, pl. 10 (fig. 7), text-fig. 64.

Type

Holotype, by original designation, is the specimen figured by Collignon (1963, pl. 291 (fig. 1269)) from locality 92–5, Mont Raynaud (Diego Suarez), Madagascar, Upper Albian, *Pervinquieria inflata* Zone.

Material

Nine specimens, SAM-PCZ6272–4, Z6277a–b, Z6278–6279, BMNH–C81264–81265, all from locality 179, sisal fields north of the Msundusi River around the pumping station 2 100 m SSW of Ndumu Store, Ndumu, northern Zululand. Recent excavations for a new road have exposed tens of metres of this section. Mzinene Formation, Albian IV.

Dimensions

<i>Specimen</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb/Wh</i>	<i>U</i>
PCZ6273	240,0	70,0 (29,2)	141,0 (58,7)	0,50	12 (5,0)
PCZ6272	288,0	75,0 (26,0)	157,0 (54,5)	0,48	11,0 (3,8)
PCZ6274 at	316,0	85,0 (26,9)	185,0 (58,4)	0,46	—
at	88,0	24,5 (27,8)	53,0 (60,2)	0,46	—
at	57,5	15,0 (26,3)	31,5 (54,8)	0,48	—
at	37,0	11,0 (29,7)	24,0 (64,9)	0,46	—
at	22,5	7,3 (32,4)	11,4 (50,7)	0,64	—
Holotype	240	80 (33)	135 (56)	0,59	27 (11)
Förster (1975)	110	28 (25)	57 (52)	0,59	8 (7)
BMNH–C81264	184,0	—	101,0 (55,0)	—	9,0 (5,0)
PCZ6277a	c. 129	—	—	—	—
PCZ6277b	c. 160	—	—	—	—

Description

Markedly dimorphic; macroconchs still septate at diameters between 200 and nearly 300 mm, and microconchs septate to a diameter of 100 mm. Macroconchs include the holotype, PCZ6262–6274, and C81264, whereas microconchs include the specimen figured by Förster (1975, pl. 10 (fig. 7), text-fig. 64) and PCZ6277a–b.

Very involute, with a tiny deep umbilicus comprising on average 5 per cent of the total diameter. The umbilical seam is characteristically undercut on the mould, with a rounded, convex umbilical wall, even on the body chamber.



Fig. 111. *Hypengonoceras decaryi* Collignon, 1963. SAM-PCZ6272. Macroconch. Note persistence of ventral clavi to relatively large diameter. $\times 0,65$.

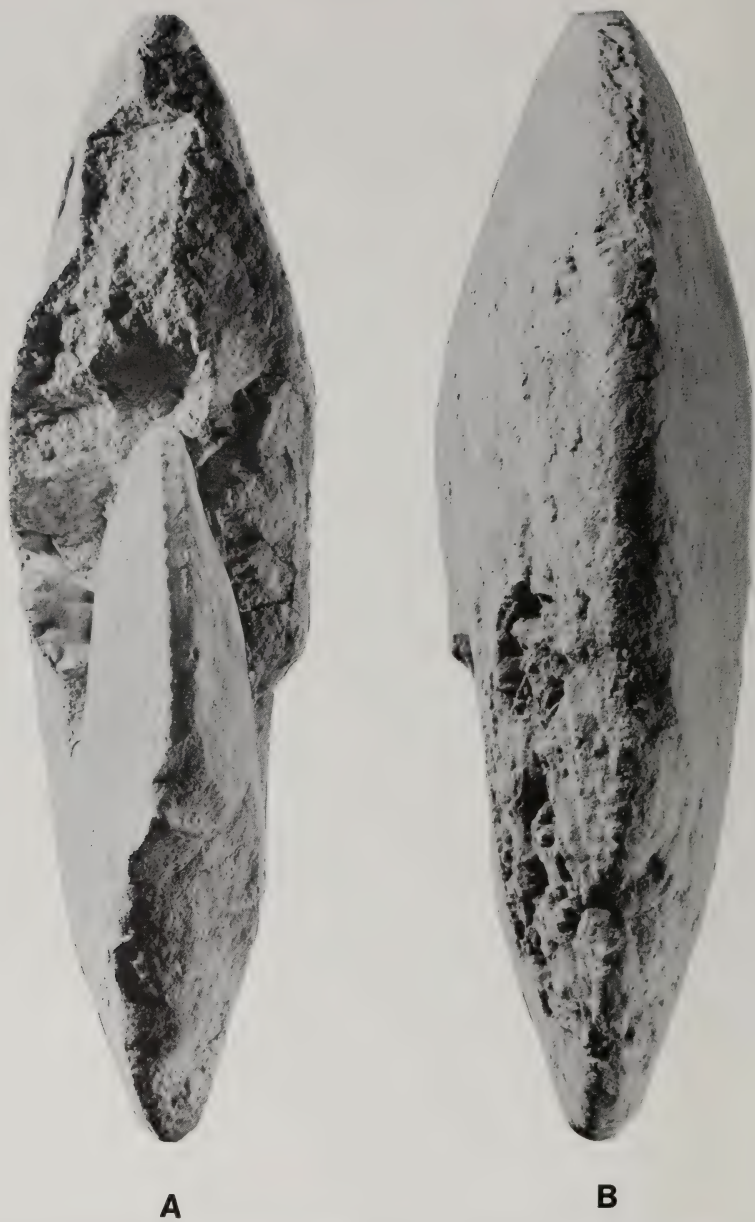


Fig. 112. *Hypengonoceras decaryi* Collignon, 1963. SAM-PCZ6272. Macroconch. $\times 0,65$.



Fig. 113. *Hypengonoceras decaryi* Collignon, 1963. SAM-PCZ6273. Macroconch. $\times 1$.

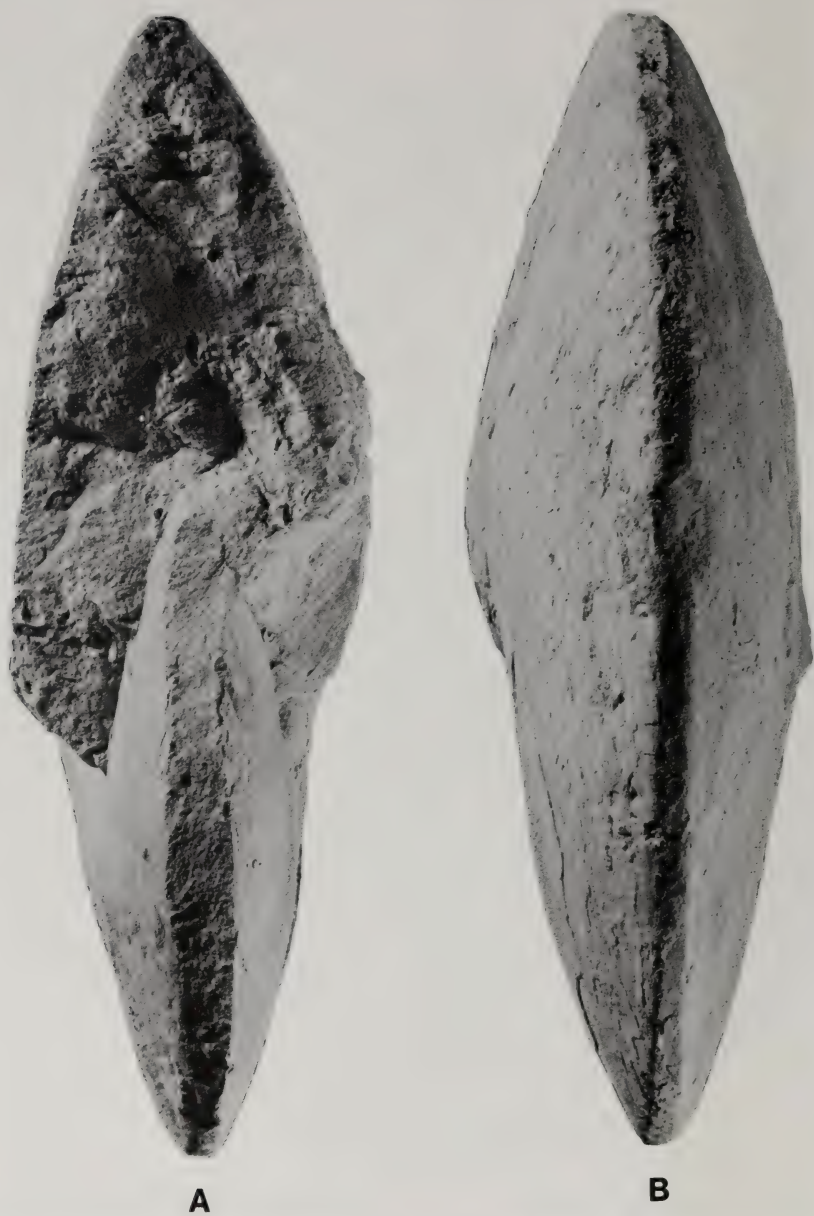


Fig. 114. *Hypengonoceras decaryi* Collignon, 1963. SAM-PCZ6273. Macroconch. $\times 1$.



Fig. 115. *Hypengonoceras decaryi* Collignon, 1963. SAM-PCZ6277. Microconch. $\times 0,87$.



Fig. 116. *Hypengonoceras decaryi* Collignon, 1963. SAM-PCZ6274. Macroconch. $\times 0,56$.



Fig. 117. *Hypengonoceras decaryi* Collignon, 1963. SAM-PCZ6274. Macroconch. $\times 0,56$.



Fig. 118. *Hypengonoceras decaryi* Collignon, 1963. SAM-PCZ6276. Macroconch. $\times 0.9$.



Fig. 119. *Hypengonoceras decaryi* Collignon, 1963. SAM-PCZ6376. Macroconch. $\times 0,9$.



Fig. 120. *Hypengonoceras decaryi* Collignon, 1963. SAM-PCZ6275. Microconch. $\times 1$.



Fig. 121. *Hypengonoceras decaryi* Collignon, 1963. SAM-PCZ6275. Microconch. $\times 1$.

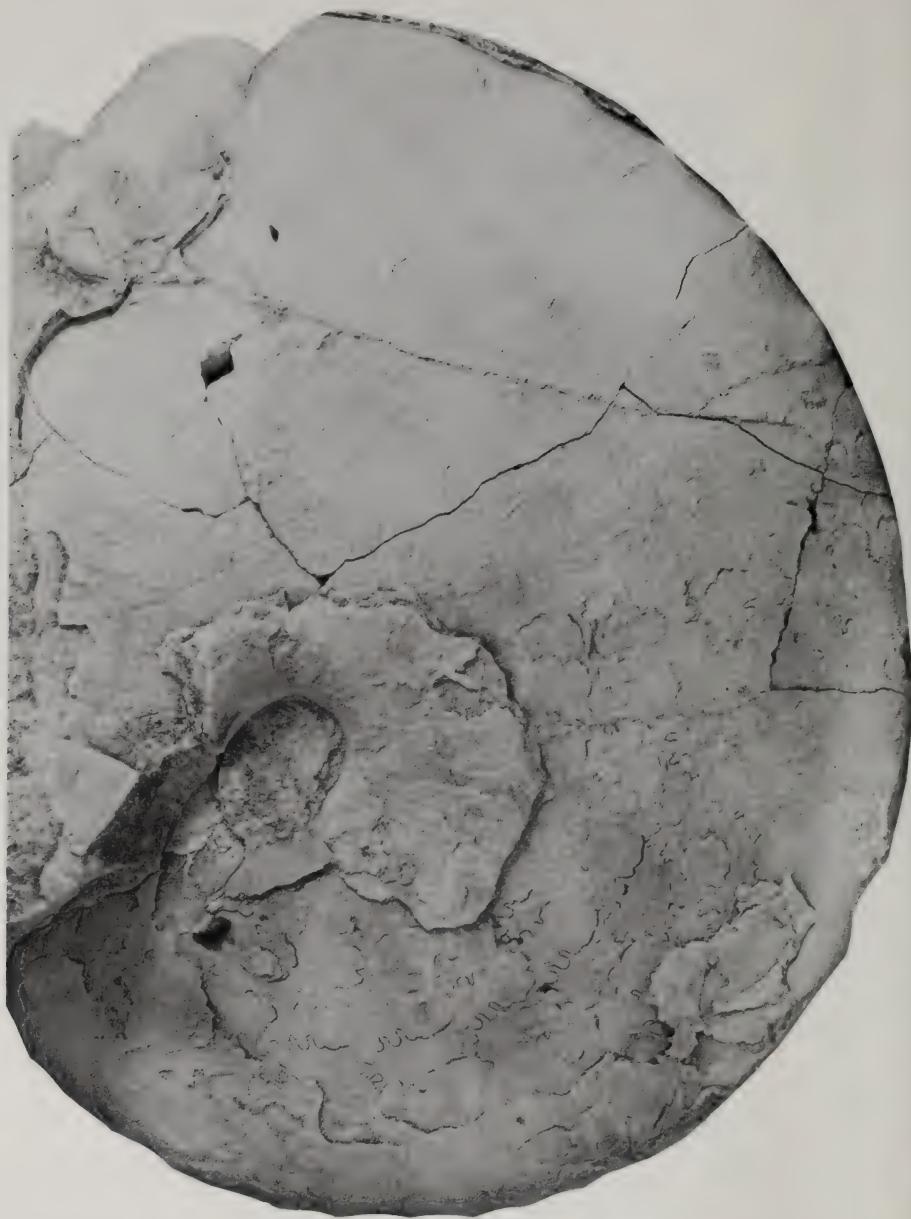


Fig. 122. *Hypengonoceras decaryi* Collignon, 1963. BMNH-C81264. Macroconch. $\times 0,9$.

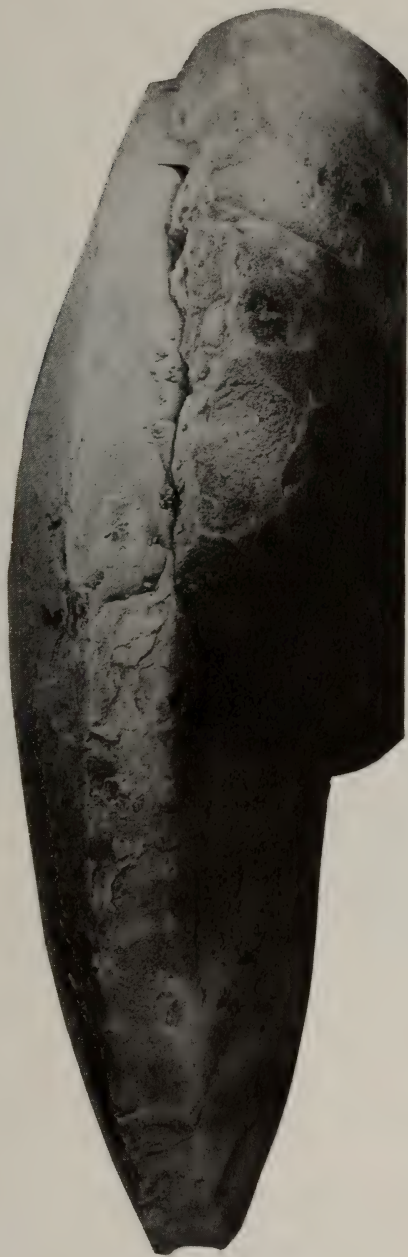


Fig. 123. *Hypengonoceras decaryi* Collignon, 1963. BMNH-C81264. Macroconch. $\times 0,9$.



Fig. 124. *Hypengonoceras decaryi* Collignon, 1963. SAM-PCZ6278. Inner whorls of macroconch showing position of umbilical tubercle. $\times 1$.

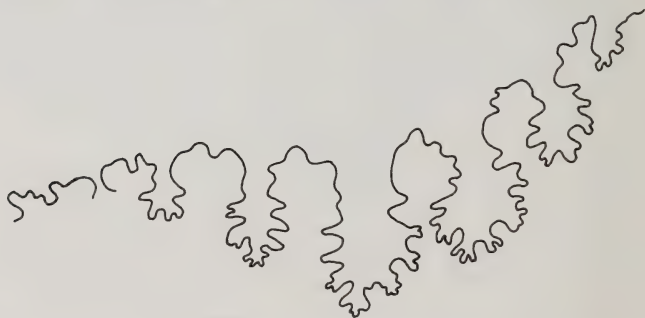


Fig. 125. *Hypengonoceras decaryi* Collignon, 1963. BMNH, unregistered specimen. Suture line. Scale bar in mm.

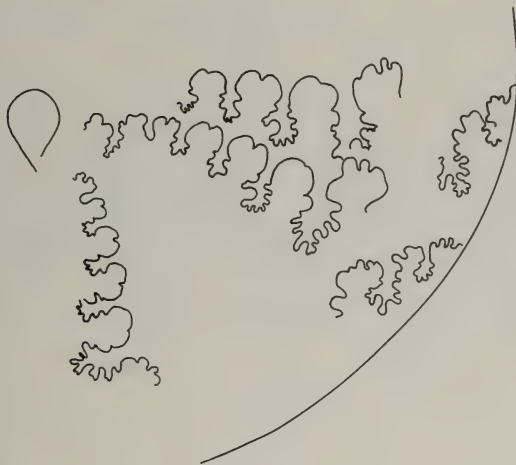


Fig. 126. *Hypengonoceras decaryi* Collignon, 1963. SAM-PCZ6273. Suture line. $\times 1$.

The whorls are compressed, tapering to a very narrow, flattened venter. Ontogenetic change in whorl section is best seen in PCZ6278 (Fig. 124) and PCZ6274 (Figs 116–117). During the ontogeny the maximum whorl breadth migrates from near the umbilical edge to near the dorsal third of the flanks.

The venter is narrow, initially rounded in the very early (embryonic) stages of growth, but then becomes concave and eventually flat on the greater part of the phragmocone, and finally slightly rounded on the body chamber.

At first glance the species appears completely devoid of lateral ornament, save fine, prorsiradiate flexuous striae. However, closer examination under oblique illumination shows obscure, low folds on the flanks of the phragmocone, especially on PCZ6272 (Figs 111–112). Examination of the inner whorls of PCZ6278 (Fig. 124) shows the impression of about four low, rounded umbilical tubercles per half whorl on the umbilical plug. The umbilical tubercles may possibly be associated with stronger ribbing, but we lack material with shell to substantiate this. This stage with umbilical tubercles persists to a diameter of about 75 mm in PCZ6278.

The body chamber is at least half a whorl in length. The sutures are extremely variable. Unfortunately the early sutural development could not be determined, but the adult suture varies from specimen to specimen at the same diameters. The lobes in PCZ6273 (Fig. 113) are rounded, with only minute central incisions—virtually ceratitic—whereas the sutures of PCZ6272 (Fig. 111) are highly denticulate and though perhaps not typically placenticeratid, certainly not ‘pincer-like Hypengonoceratid’.

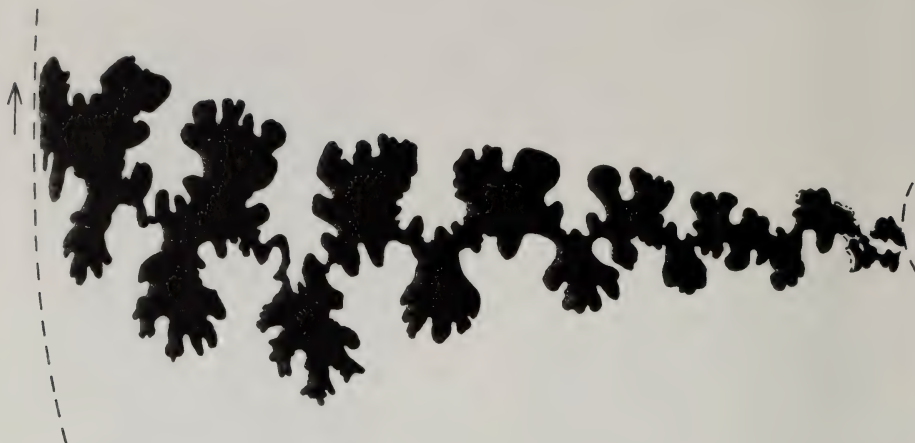


Fig. 127. Suture line of *Hypengonoceras chouberti* Collignon, 1966. (After Collignon 1966, pl. 5.)

Discussion

The Zululand material differs from Collignon's (1963) holotype in generally having a much smaller umbilicus, but is similar in having a very compressed, trigonal whorl section and virtually smooth flanks. Given the range of intraspecific variation in other ammonites, these differences are rather trivial. The species is of great interest in demonstrating dimorphism in *Hypengonoceras*.

In view of the considerable intraspecific variation, comparison with other described species is difficult: *H. warthi* (Kossmat) has low, broad, falcoid ribs at diameters comparable to the Zululand material; *H. chouberti* Collignon is smooth, more compressed, with well-developed keels on the ventral shoulders bearing tiny clavi; *H. tarfayense* Collignon is a smooth, slender species, with a very narrow venter and tiny umbilicus and an ornament of fine dense costules on the flank. As far as is known, none of these species has umbilical tubercles at any stage of growth, thus differing from the Zululand material.

Occurrence

Upper Albian of Zululand, Mozambique and Madagascar.

SPECULATIONS ON INTRASPECIFIC VARIATION IN
PLACENTICERATIDAE

Description of the Zululand faunas and work on large collections of placenticeratids from other areas has clearly demonstrated the considerable extent of intraspecific variation (e.g. Hyatt 1903; Reeside 1927*b*; Wolleben 1967; Kennedy & Wright 1983). This raises the question why this intraspecific variation is so widespread in the Placenticeratidae and, for that matter, most of the other known Cretaceous narrowly umbilicate, compressed taxa, e.g. Engonoceratidae, *Pseudoschloenbachia* (Collignon 1969; unpublished data Zululand), *Eulophoceras* (unpublished data Zululand), *Submorticeras* (Klinger & Kennedy 1980*a*), etc.

Arnould-Saget (1956) attempted to explain the extreme intraspecific variation in *Knemiceras* from southern Tunisia. Here both ornament and suture lines are very variable. According to her, the variations are individual and irrational; their systematic study is sterile from an evolutionary point of view, and variation is ascribed to palaeobiological causes. The Tunisian *Knemiceras* lived in a stable environment in the neritic zone at the margins of the old Saharan mainland, without important detritus deposits and without violent perturbation. These optimum conditions did not create any need for adaptation; the life potential of *Knemiceras* wasted itself in a useless and directionless polymorphism, but also underlines the mode of life of these animals—more benthonic than neritic! Thus Arnould-Saget.

In Zululand, *Placenticeras kaffrarium* occurs in a transgressive environment, following regression and/or non-deposition and erosion during the Upper Cenomanian and Turonian. Associated ammonite faunas consist mainly of heteromorphs, e.g. *Bostrychoceras*, *Scaphites*, *Allocrioceras*, abundant *Baculites*, *Pseudoxybeloceras*, and evolute forms of *Peroniceras*—*P. (P.) lepeei* and *P. (P.) tridorsatum*, and ornate *Forresteria*. Apart from the absence of complete apertures in the placenticeratids, preservation of all these forms is superb, often with the original nacre present. This all is indicative of a near-shore, protected environment with absence of strong currents and wave action but, nevertheless, normal salinity.

As we have demonstrated, coiling in most placenticeratids remains virtually unchanged throughout their evolutionary history from the Cenomanian to the Maastrichtian, i.e. narrowly umbilicate compressed. With rare exceptions (e.g. the Jurassic Amaltheidae—Howarth 1958; Kennedy 1977) oxyconic coiling seems to be a unidirectional evolutionary 'cul-de-sac' (e.g. *Submorticeras*—Klinger & Kennedy 1980*a*; *Peroniceras* (*Zuluites*)—Klinger & Kennedy 1984). The only noticeable, albeit slow and gradual trend in most of the Placenticeratidae, is the acquisition of lateral ornament at the expense of umbilical ornament.

Instead of regarding the variation in *Placenticer*as as useless and directionless and coupled to a semi-benthonic mode of life, as suggested by Arnould-Saget (1956), Chamberlain & Westermann (1976) suggested that the ornamentation in ammonite shell morphotypes like those of *Placenticer*as may in fact have been related to an active, nektonic mode of life, and to have been of hydrodynamic significance. There is thus a distinct relationship between lateral ornament and shell diameter, especially in compressed forms. To minimize drag, compressed species with adult diameters of about 100 cm should become progressively smoother during growth. The juveniles would be favoured if they had ornamented shells. In contrast, the opposite trend would be of advantage in species with adult diameters of 10 to 20 cm. This is what is seen in the most common form of dimorphism in *Placenticer*as. The macroconchs are generally much more weakly ornamented than the microconchs on the outer whorls. This does not, however, explain in functional terms why some forms retain the smooth '*umkwelanense*'-type of ornament up to the adult stage, whereas others are already ornate at small diameters. It is also interesting to note that, according to Chamberlain & Westermann (1976), all drag-producing ornament is located on the flanks. Ornament on the umbilicus has little drag-producing effect. This may be perhaps why umbilical ornament is gradually diminished in some placenticeratids, or tends to migrate outwards during growth, thus producing extra drag.

LIST OF DESCRIBED SPECIES REFERRED TO PLACENTICERATIDAE

In view of the wide intraspecific variation shown by placenticeratid species, detailed synonymies are difficult to compile, except where large populations are available. We merely list species described. Lectotypes are designated where necessary. These are indicated by *.

Genus *Placenticer*as

*Placenticer*as *aktaschensis* (Iljin, 1975) (p. 159, pl. 32 (figs 2-3), pl. 33 (fig. 4)).
Cenomanian of Central Asia.

*Placenticer*as *ambai* (Chiplonkar & Ghare, 1976) (p. 3, pl. 1 (figs 1, 4), text-figs 2-3). Presumably Upper Albian to Cenomanian of India.

*Placenticer*as *asiaticum* (Iljin, 1975) (p. 156, pl. 31 (fig. 2a-b), pl. 33 (fig. 2)).
Cenomanian of Central Asia.

*Placenticer*as *baghensis* (Chiplonkar & Ghare, 1976) (p. 4, pl. 1 (figs 3-6)).
Presumably Upper Albian to Cenomanian of India.

*Placenticer*as *beliakovae* (Iljin, 1975) (p. 160, pl. 33 (fig. 1), pl. 34 (fig. 5)).
Cenomanian of Central Asia.

*Placenticer*as *benningi* Stephenson, 1956 (p. 247, pl. 44 (figs 21, 22), pl. 45 (figs 7-11)).

*Placenticer*as *besairiei* (Collignon, 1936) (Collignon 1965b: 19, pl. 383 (fig. 1650)). Middle Turonian of Madagascar. (? = *Placenticer*as *kaffrarium*)

- Placenticerias beschubensis* (Iljin, 1975) (p. 163, pl. 29 (figs 1–2), pl. 39 (fig. 7)). Turonian of Central Asia.
- Placenticerias bidorsatum* (Roemer, 1841) (p. 88, pl. 13 (fig. 8)). Lower Campanian of Germany.
- Placenticerias blanfordi* (Chiplonkar & Ghare, 1977a) (p. 73, pl. 1 (fig. 3)). Cenomanian–Turonian of India.
- Placenticerias bobkova* Iljin, 1975 (p. 169, pl. 31 (fig. 1), pl. 35 (fig. 12)). Santonian of Central Asia.
- Placenticerias canaliculatum* Hyatt, 1903 (p. 243). Lower Campanian of Germany. (Objective synonym of *P. bidorsatum* Roemer, 1841, *vide* Kennedy 1986).
- Placenticerias carteri* (Chiplonkar & Ghare, 1977a) (p. 70, pl. 2 (fig. 1), text-fig. 1). Cenomanian–Turonian of India.
- Placenticerias colquitti* Wollebein, 1967 (p. 1164, pl. 150 (figs 1–4), text-fig. 8e). Santonian of Texas.
- Placenticerias crassatum* Hyatt, 1903 (p. 24). Lower Senonian of Germany. (= *Placenticerias polyopsis* (Dujardin))
- Placenticerias cummingsi* Cragin, 1893 (p. 237). Late Cenomanian, New Mexico (Cobban 1983a), Texas.
- Placenticerias dangerfieldi* (Chiplonkar & Ghare, 1977a) (p. 69, pl. 1 (fig. 2)). Cenomanian–Turonian of India.
- Placenticerias fourtaui* (Chiplonkar & Ghare 1977a) (p. 73, pl. 1 (fig. 1)). Cenomanian–Turonian of India.
- Placenticerias fritschii* de Grossouvre, 1894 (p. 124, pl. 5 (figs 1–2), text-fig. 52). Coniacian of France, Czechoslovakia (Fritsch & Schloenbach 1872), and India (Chiplonkar & Ghare 1977a).
- Placenticerias gaurdakense* (Luppov, 1963) (p. 144, pl. 1 (fig. 1)). Middle Cenomanian of Central Asia.
- Placenticerias gissarensis* (Iljin, 1975) (p. 155, pl. 31 (fig. 1a–b), pl. 33 (fig. 1)). Cenomanian of Central Asia.
- Placenticerias grossouvrei* Hyatt, 1903 (p. 237). Santonian of France. (= *Placenticerias polyopsis* (Dujardin))
- Placenticerias grossouvrei* Semenov, 1899 (p. 97, pl. 2 (fig. 5)). Cenomanian of Transcaspia. (*non Placenticerias grossouvrei* Hyatt, 1903)
- Placenticerias guadalupae* (Roemer, 1852) (p. 32, pl. 2 (fig. 1)). Campanian of Germany (Riedel 1937), New Mexico, Texas, U.S. Western Interior (Reese 1927b). (= *Placenticerias syrtale* (Morton, 1834))
- Placenticerias helicus* (Chiplonkar & Ghare, 1977a) (p. 74, pl. 2 (figs 3–4)). Cenomanian–Turonian of India.
- Placenticerias hispanicum* (Mas & Wiedmann, 1980) (p. 267, figs 4–5). Middle Cenomanian of Spain.
- Placenticerias hyatti* Diener, 1925 (p. 185). Santonian of France. (= *Placenticerias polyopsis* (Dujardin, 1837))
- Placenticerias iljini* (Khakimov, 1976) (*in* Atabekian & Khakimov 1976: 93, pl. 10 (fig. 1)). Lower Campanian of Central Asia.

- Placenticerus incisum* Hyatt, 1903 (p. 238). Santonian of France. (= *Placenticerus polyopsis* (Dujardin))
- Placenticerus intercalare* (Meek & Hayden, 1860) (p. 117). Campanian of North America and possibly Germany (Riedel 1937).
- Placenticerus intermedium* Johnson, 1903 (p. 206, pl. 8 (fig. 27)). Upper Santonian–Lower Campanian of New Mexico. (= *Placenticerus syrtale* (Morton))
- Placenticerus kaffrarium* Etheridge, 1904 (p. 89, pl. 3 (fig. 16)). Coniacian of Zululand, offshore Alaphard Group, Madagascar, Angola, ?South West Africa–Namibia, and probably India.
- Placenticerus keatingi* (Chiplonkar & Ghare, 1977a) (p. 71, pl. 2 (fig. 2), text-fig. 2). Cenomanian–Turonian of India.
- Placenticerus kharesmense* (Lahusen, 1884) (Archanguelski 1916: 40, pl. 6 (fig. 5), pl. 7 (fig. 1)). Turonian of Turkestan.
- Placenticerus kolbajense* (Sokolov, 1967) (p. 138, text-fig. p. 139). Upper Albian of Central Asia.
- Placenticerus kossmati* (Chiplonkar & Ghare, 1979) (p. 131, pl. 1 (figs 1–3), pl. 2 (fig. 1)). Upper Turonian–Coniacian of India.
- Placenticerus kotzi* (Iljin, 1975) (p. 165, pl. 30 (figs 1–2), pl. 39 (fig. 9)). Coniacian of Central Asia.
- Placenticerus kutuzovae* (Iljin, 1975) (p. 164, pl. 29 (fig. 3), pl. 39 (fig. 8)). Turonian of Central Asia.
- Placenticerus kysylchense* (Iljin, 1958) (p. 728, figs 1a–b, 2d–e). Maastrichtian of Uzbekistan.
- Placenticerus kysylcumense* Archanguelski, 1916 (p. 45, pl. 7 (figs 4–7), text-fig. 16). Turonian of Turkestan.
- Non Placenticerus liardense* Whiteaves, 1889 (p. 150, pl. 20 (figs 1–2)). Upper Cretaceous of Canada. (= *Paragastrolites*—*fide* Imlay 1961: 63)
- Placenticerus luppovi* Iljin, 1975 (p. 170, pl. 32 (fig. 1), pl. 35 (fig. 13)). Santonian of Central Asia.
- Placenticerus maherndli* Summesberger, 1979 (p. 155, pl. 14 (figs 58–61), pl. 15 (figs 62–66), text-figs 40–47). Upper Santonian of Austria.
- Placenticerus meeki* Boehm, 1898 (p. 200). Upper Senonian of North America (Hyatt 1903; Reeside 1927a).
- Placenticerus meeki* var. *tuberculata* Hyatt, 1903 (p. 232, pl. 47 (fig. 5)). Upper Senonian of Dakota.
- Placenticerus memoriaschloenbachi* Laube & Bruder, 1887 (p. 221, pl. 23 (fig. 1)). Cenomanian–Turonian of Bohemia and Saxony, France (Kennedy *et al.* 1981).
- Placenticerus memoriaeschloenbachi* Laube & Bruder var. *ambiloensis* Collignon, 1965 (Collignon 1965a: 14, 16, pl. 381 (figs 1646), pl. 382 (1647–8)). Turonian of Madagascar and India (Chiplonkar & Ghare 1977a). (= *Placenticerus kaffrarium* Etheridge, 1904)

- Placenticerus merenskyi* Haughton, 1930 (p. 363, pl. 11 (figs 1–3)). Cenomanian? of South West Africa–Namibia.
- Placenticerus milleri* von Hauer, 1866 (p. 5, pl. 2 (figs 1–2)). Coniacian–Santonian of northern Alps and Gosau Beds, and tentatively India (Chiplonkar & Ghare 1977a).
- Placenticerus mintoi* Vredenburg, 1907 (p. 111, pls 14–15). Cenomanian of Bagh, India (Chiplonkar & Ghare 1977a). (= ?*Knemiceras*)
- Placenticerus murphyi* (Collignon, 1965a) (p. 17, pl. 382 (fig. 1649)). Upper Turonian of Madagascar. (= ?*Placenticerus kaffrarium* Etheridge)
- Placenticerus newberryi* Hyatt, 1903 (p. 203, pl. 31 (figs 3–5)). Upper Cretaceous, New Mexico, Western Interior (Reeside 1927a). (= *Placenticerus syrtale* (Morton, 1834))
- Placenticerus orbignyanum* (Geinitz, 1849) (p. 114, pl. 4 (fig. 1)). Coniacian of N. Germany, Czechoslovakia and Madagascar. (= ?*Placenticerus fritschi* de Grossouvre)
- Placenticerus ornatus* (Chiplonkar & Ghare, 1977a) (p. 72, pl. 1 (fig. 5)). Cenomanian–Turonian of India.
- Placenticerus paraplunum* Wiedmann, 1978 (p. 666, pl. 1 (figs 3–4), text-fig. 2a). Santonian of the Gosau Beds, Austria, France (Amedro & Hancock 1985; Kennedy 1987).
- Placenticerus patagonicum* Leanza, 1967 (p. 16, pl. 1 (figs 1–2), pl. 2 (fig. 1), pl. 3 (figs 1–3), pl. 4 (figs 2–3), pl. 9 (figs 1–5), pl. 10 (fig. 3)). Allegedly Lower Campanian of Patagonia. (Turonian—pers. observation H.C.K.)
- Non Placenticerus perezianum* (Whiteaves, 1876) (p. 19, pl. 2 (fig. 1)). Lower Cretaceous British Columbia, Canada. (= *Cleonicerus* (*Grycia*)—*fide* McLearn 1972: 59)
- Placenticerus pitniakense* Iljin, 1975 (p. 167, pl. 32 (fig. 2), pl. 35 (fig. 11)). Coniacian of Central Asia.
- Placenticerus placenta* (DeKay, 1828) (p. 278, pl. 5 (fig. 2)). Upper Cretaceous, New Jersey, Alabama, U.S.A., Turkestan (Archanguelski 1916).
- Placenticerus planum* Hyatt, 1903 (p. 202, pl. 33 (figs 2–4)). Upper Cretaceous, Texas, U.S.A. (Reeside 1927a), and tentatively India (Chiplonkar & Ghare 1977a). (= *Placenticerus syrtale* (Morton, 1834))
- Placenticerus polyopsis* (Dujardin, 1837) (p. 232, pl. 17 (fig. 12)). Santonian of France, Austria, Germany, and possibly Alabama, U.S.A.
- Placenticerus polyopsis amudariense* (Iljin, 1975) (p. 171, pl. 32 (fig. 3), pl. 35 (fig. 14)). Santonian of Central Asia. (? = *Placenticerus polyopsis* s.s.)
- Placenticerus proplanum* (Iljin, 1975) (p. 166, pl. 37 (fig. 2), pl. 35 (fig. 10)). Coniacian of Central Asia.
- Placenticerus pseudocostatum* Johnson, 1903 (p. 137, pl. 10 (fig. 29a), pl. 11 (fig. 29b–c)). Upper Santonian–Lower Campanian, New Mexico. (= *Placenticerus syrtale* (Morton, 1834))
- Placenticerus pseudorbignyanum* Hyatt, 1903 (p. 242). Santonian of northern Germany.

- Placenticerias pseudoplacenta* Hyatt, 1903 (p. 216, pl. 43 (figs 3–11), pl. 44). Upper Cretaceous of Utah, Minnesota, U.S.A. (Cobban 1983*b*—as *Placenticerias cumminsi* Cragin, 1893), ?Palestine (Taubenhaus 1920), Oregon (Reeside 1927*a*).
- Placenticerias pseudoplacenta* var. *occidentalis* Hyatt, 1903 (p. 217 (*pars*), pl. 45 (fig. 2 only)). Cenomanian of Texas, U.S.A. (= *Placenticerias cumminsi* Cragin, 1893)
- Placenticerias radiatum* Riedel, 1937 (p. 219, pl. 16 (figs 1–2)). Santonian of Germany. (= *Placenticerias polyopsis* (Dujardin, 1837))
- Placenticerias rampuraensis* (Chiplonkar & Ghare, 1977*c*) (p. 109, figs 1–2, 6A, D). Turonian of India.
- Placenticerias reineckeii* Haughton, 1925 (p. 271, pl. 13 (figs 4–5)). Upper Turonian of Angola. (= ?*Placenticerias kaffrarium* Etheridge, 1904)
- Placenticerias ribourianus* (d'Orbigny, 1850) (p. 213). Santonian of France. (= *Placenticerias polyopsis* (Dujardin, 1837))
- Placenticerias rotundatum* Johnson, 1903 (p. 135, pl. 9 (figs 28*a*–*b*)). Upper Santonian–Campanian of New Mexico. (? = *Placenticerias syrtale* (Morton, 1834))
- Placenticerias rooneyi* Wolleben, 1967 (p. 1164, pl. 150 (figs 6–7), pl. 151 (figs 3–4) pl. 152 (figs 33–34), text-fig. 7*d*–*g*). Upper Santonian–Lower Campanian of Texas and New Mexico, U.S.A.
- Placenticerias saggitalis* (Iljin, 1975) (p. 161, pl. 33 (fig. 2), pl. 34 (fig. 6)). Cenomanian of Central Asia.
- Placenticerias sancarlosense* Hyatt, 1903 (p. 200, pl. 30 (figs 1–3), pl. 31 (figs 1–2)). Upper Santonian–Lower Campanian of Texas, and Western Interior, U.S.A (Reeside 1927*a*). (= *Placenticerias syrtale* (Morton, 1834))
- Placenticerias sancarlosense* var. *pseudosyrtale* Hyatt, 1903 (p. 200, pl. 32, pl. 33 (fig. 1)). Upper Santonian–Lower Campanian of Texas, New Mexico, and Western Interior, U.S.A (Reeside 1927*a*).
- Placenticerias sanctacrucense* Leanza, 1967 (p. 15, pl. 8 (fig. 2), pl. 4 (fig. 1)). Allegedly Lower Campanian of Patagonia (Turonian—pers. observation H.C.K.).
- Placenticerias satriense* (Collignon, 1965*b*) (p. 40, pl. 431 (fig. 1782)). Upper Coniacian of Madagascar. (= ?*Placenticerias kaffrarium* Etheridge)
- Placenticerias schlüteri* Hyatt, 1903 (p. 239). Santonian of northern Germany.
- Placenticerias semiornatum* (d'Orbigny, 1850) (p. 212). Upper Coniacian–Santonian of France (Kennedy 1984).
- Placenticerias simonyi* Kossmat, 1907 (p. 49, pl. 4 (fig. 1)). Cenomanian of Sokotra.
- Placenticerias spathi* (Chiplonkar & Ghare 1977*c*) (p. 110, fig. 7*E*–*F*). Turonian of India.
- Placenticerias spillmanni* Hyatt, 1903 (p. 233, pl. 47 (figs 6–8)). Upper Cretaceous of New Jersey and Mississippi, U.S.A.

- Placenticerias stantoni* Hyatt, 1903 (p. 214). Upper Cretaceous of Utah and Minnesota, U.S.A. (Cobban 1983b), and ?India. (= *Placenticerias cumminsi* Cragin)
- Placenticerias stantoni* var. *bolli* Hyatt, 1903 (p. 214, pl. 40 (figs 3–7), pls 41–42, 43 (figs 1–2)). Upper Cretaceous of Texas, U.S.A., ?Upper Turonian of Madagascar and ?India (Chiplonkar & Ghare 1977a). (= *Placenticerias cumminsi* Cragin) (Chiplonkar & Ghare 1977a)
- Placenticerias stantoni* var. *fortior* (Collignon, 1965a) (p. 19, pl. 383 (fig. 1652)). Turonian of Madagascar. (? = *Placenticerias kaffrarium* Etheridge)
- Placenticerias stoliczkai* (Chiplonkar & Ghare, 1979) (p. 131, pl. 2 (fig. 2), pl. 3 (figs 1–2)). Turonian–Coniacian of India.
- Placenticerias subkaffrarium* Spath, 1921 (p. 247, pl. 21 (fig. 2)). Coniacian of Zululand and Madagascar. (= *Placenticerias kaffrarium* Etheridge)
- Non Placenticerias subplanatum* Taubenhaus, 1920 (p. 40, pl. 7 (fig. 2), pl. 8 (fig. 4)). Upper Cretaceous of Palestine. (Not a placenticeratid—*Coilopoceras* ?)
- Placenticerias syrtale* (Morton, 1834) (p. 40, pl. 16 (fig. 4)). Upper Santonian–Lower Campanian of U.S. Gulf Coast and Rocky Mountain areas (Reeside 1927a).
- Placenticerias syrtale adkinsi* Wolleben, 1967 (p. 1164, pl. 151 (figs 8–9), pl. 152 (figs 1–2, 5–8), text-fig. 8g). Upper Santonian–Lower Campanian of Texas and New Mexico.
- Placenticerias syrtale costata* Riedel, 1931 (p. 696, pl. 79 (fig. 2)). Santonian of Germany. (= *Placenticerias polyopsis* (Dujardin))
- Placenticerias syrtale* var. *halei* Hyatt, 1903 (p. 206, pl. 27 (figs 16–17), pl. 28 (figs 3–6)). Upper Cretaceous of Alabama, U.S.A.
- Placenticerias tamulicum* (Blanford, 1862) (p. 118). Upper Turonian–Coniacian of India and Madagascar.
- Placenticerias telifer* (Morton, 1834) (p. 38, pl. 2 (fig. 7)). Senonian of New Jersey, U.S.A.
- Placenticerias vancouverense* (Meek, 1876) (p. 370, pl. 6 (fig. 1)). Upper Cretaceous of British Columbia, Canada and Sucia Island, U.S.A. (= ?*Hoplitoplacenticerias*)
- Placenticerias viedmaense* Leanza, 1967 (p. 12, pl. 4 (figs 1–3), pl. 8 (fig. 1), pl. 10 (fig. 1e)). Allegedly Lower Campanian of Patagonia (Turonian—pers. obs. H.C.K.).
- Placenticerias vredenburgi* (Sarkar, 1966) (p. 144, pl. 11 (figs 1–2)). Turonian–Coniacian of India (Chiplonkar & Ghare 1977a).
- Placenticerias washbournei* Leanza, 1967 (p. 17, pl. 5 (fig. 1), pl. 10 (fig. 4)). Allegedly Lower Campanian, Patagonia (= Turonian—pers. obs. H.C.K.).
- Placenticerias whitfieldi* Hyatt, 1903 (p. 222, pl. 45 (figs 3–16), pls 46, 47 (figs 1–4)). Upper Cretaceous of Nebraska, South Dakota and Colorado, U.S.A. (= *Placenticerias meeki* Böhm)

- Placenticerus ?yakounense* (Whiteaves, 1900) (p. 280, pl. 36 (figs 1, 1a-b)). Upper Cretaceous of Canada. (= *?Hoplitolacenticerus*)
- Placenticerus* n. sp. aff. *kaffrarium* Etheridge: Venzo, 1936 (p. 108 (50), pl. 11 (7) (fig. 13)). Coniacian of Zululand and Madagascar (= *Placenticerus kaffrarium* Etheridge)
- Non Placenticerus zehariense* (Collignon, 1966) (p. 33, pl. 18 (figs 5-9)). Turoonian of Morocco. (= *?Hoplitoides*—fide Cobban & Hook 1980)

Genus and subgenus *Hoplitolacenticerus* Paulcke, 1907

- **Hoplitolacenticerus antokazoense* Collignon, 1970 (pp. 76, 80, pl. 638 (fig. 76), pl. 639 (fig. 2354))—the latter herein designated lectotype. Upper Campanian of Madagascar.
- Non Hoplitolacenticerus awadi* Hassan, 1971 (p. 71, pl. 2 (figs 8-9)). Lower Maastrichtian of Egypt (= scaphitid).
- **Hoplitolacenticerus besairiei* Collignon, 1970 (p. 77, pl. 638 (figs 2349-50))—figure 2349 herein designated lectotype. Upper Campanian of Madagascar.
- Hoplitolacenticerus coesfeldiense* var. *schlüteri* Michailov, 1951 (p. 82, pl. 15 (figs 60-61)). Upper Campanian of Don Basin, U.S.S.R., Westphalia, F.G.R., and Wyoming, U.S.A. (Cobban 1963).
- Hoplitolacenticerus coesfeldiense* (Schlüter, 1867) (p. 14, pl. 1 (figs 1, 4-5)). Upper Campanian of Germany (Giers 1964), European Russia (Michailov 1951), Central Asia (Atabekian & Khakimov 1976), Caucasus, Crimea (Naidin & Shimanskij 1959), and Ukraine (Naidin 1974), Sweden (Ødum 1953), and France (Kennedy 1986).
- Hoplitolacenticerus costulosum* (Schlüter, 1867) (p. 17, pl. 2 (figs 2-4)). Upper Campanian of Germany and, tentatively, Madagascar.
- Hoplitolacenticerus dolbergense* (Schlüter, 1876) (p. 159, pl. 44 (figs 1-4)). Upper Campanian of Germany (Giers 1964; Schmid & Ernst 1975), tentatively Madagascar (Collignon 1971), and France (Kennedy 1986).
- Hoplitolacenticerus fugen* Matsumoto, 1984 (p. 25, pl. 8 (fig. 5)). Upper Campanian of Hokkaido.
- Hoplitolacenticerus gosseti* (de Grossouvre, 1894) (p. 116, pl. 36 (fig. 1)). Upper Cretaceous of France.
- Hoplitolacenticerus howarthi* Collignon, 1970 (p. 80, pl. 639 (fig. 2351)). Upper Campanian of Madagascar.
- Non Hoplitolacenticerus kambysis* (Quaas, 1902) (p. 309, pl. 29 (figs 8-11))—as *?Scaphites kambysis*). Lower Maastrichtian of Egypt. (It is a scaphitid.)
- Hoplitolacenticerus marroti* (Coquand, 1859) (p. 995). (De Grossouvre 1894: 118, pl. 8 (fig. 3), pl. 9 (figs 2-3)). Upper Campanian of France?, Angola, Germany (Howarth 1965: 391, pl. 12 (fig. 3), pl. 13 (fig. 3)) and Madagascar (Collignon 1970: 80, pl. 639 (fig. 2353)).

- Hoplitoplacenticer* *monju* Matsumoto, 1982a (p. 249, figs 1–2). Upper Campanian of Hokkaido.
- Hoplitoplacenticer* *praematura* (Imkeller, 1901) (p. 58, fig. 1). Upper Campanian of Germany.
- Hoplitoplacenticer* *rarecostatum* Khakimov, 1976 (in Atabekian & Khakimov 1976: 88, pl. 10 (fig. 5)). Upper Campanian of Central Asia.
- Hoplitoplacenticer* *rejaudryi* (de Grossouvre, 1894) (p. 78, pl. 7 (figs 1–5), pl. 14 (figs 6–75)). Upper Campanian of France.
- Hoplitoplacenticer* *trangahyense* Collignon, 1970 (p. 76, pl. 638 (fig. 2347)). Upper Campanian of Madagascar.
- Hoplitoplacenticer* *vancouverense* (Meek, 1861) (Usher 1952: 93, pl. 25 (figs 1–2), pl. 31 (figs 21–22)). Upper Campanian of British Columbia.
- Non Hoplitoplacenticer* *yakounensis* (Whiteaves, 1900) (p. 280, pl. 36 (fig. 1, 1a–b)). Upper Campanian of Canada. (= *Anahoplites*—*fide* McLearn 1972: 57)

Subgenus *Lemfoerdicer* Kennedy, 1986

- Hoplitoplacenticer* (*L.*) *lafresnayanum* (d'Orbigny, 1842) (p. 326, pl. 97 (figs 3–5)). Upper Maastrichtian of France.
- Hoplitoplacenticer* (*L.*) *lemfoerdense* (Schlüter, 1872) (p. 160, pl. 19 (figs 1–2), pl. 44 (figs 8–9)). Upper Campanian of Germany.

Genus *Metaplacenticer* Spath, 1926

- Metaplacenticer*? *bowersi* Anderson, 1958 (p. 255, pl. 70 (figs 3–4)). Upper Campanian of California.
- Metaplacenticer* *californicum* (Anderson, 1902) (p. 78, pl. 8 (figs 173–177)). Upper Campanian of California (Anderson 1958: 254, pl. 36 (fig. 1)).
- Metaplacenticer* *pacificum* (Smith, 1900) (p. 207, pls 26–28). Upper Campanian of California (Anderson 1902: 79, pl. 8 (figs 162–164), pl. 9 (fig. 180); 1958: 254, pl. 37 (figs 1–4)).
- Metaplacenticer* *sanctaemonicae* (Waring, 1917) (p. 70, pl. 9 (figs 20–21)). Upper Campanian of California (Anderson 1958: 255).
- Metaplacenticer* *subtilstriatum* (Jimbo, 1894) (p. 171, pl. 17 (fig. 1)). Upper Campanian of Hokkaido.

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APPENDIX

ORIGINAL DIAGNOSES OF GENERA HERE PLACED IN THE SYNONYMY OF *PLACENTICERAS*

Karamaiceras Sokolov, 1967: 138

Name of the genus from the mouth of the Karamai to the east of Mangyshlak.

Type species. *K. kolbajense* sp. nov., Upper Albian, zone of *Stoliczkaia dispar* (Vraconnian); East Mangyshlak.

Diagnosis

Shell involute, discoidal, formed by high, strongly convoluted whorls. Whorl section in the species is a high, narrow triangle with truncated apex and weakly convex flanks. Umbilicus is rather narrow, deep, funnel-like with steep walls and a sharp edge. Ornament is represented by compressed, weakly s-shaped, curved ribs, umbilical and marginal tubercles. Suture line consists of shallow bulb-shaped lobes and low, wide, rounded saddles. Ventral lobe is short, the umbilical (one) is sharply asymmetric. The base of the latter has a kind of wide sinus with two relatively short branches; the inner one of which is longer than the outer. The second lobe which divides the first lateral saddle attains the length of the outer branch of the umbilical lobe.

Species composition. Type species.

Comparison

The new genus is distinguished from the closest genus *Placenticer* by the development of the suture line.

(Free translation from original Russian.)

Turkmenites Iljin, 1975: 154–155

Type species. *Placenticeras gaurdakensis* Luppov, 1963, from the Lower Cenomanian of Central Asia (Luppov 1963: 144, pl. 1 (figs 1, 2)).

Diagnosis

Shells are compressed with narrow, funnel-shaped umbilicus, smooth venter and slightly curved flanks. The umbilical tubercles are mammiform, pointed on the shell and blunt on internal casts. The external tubercles are elongated longitudinally.

The ribs are always sickle-shaped, the most prominent are on the outer part of the flanks. The surface of the shell is covered with fine sickle-shaped striae. The lobes are strongly separated by means of asymmetrical bases of the first three and by a wide, denticulated base at the posterior. The first lobe is always slanted towards the second. The fourth lobe is very small, smaller by far than the fifth lobe. The transformation of the first umbilical lobe comes about by means of formation at its base, and later on the inner sides of the lobes and incisions, along with their subsequent complete separation and transformation into independent lobes. On the first whorl, in the base of the first umbilical lobe, two notches arise of which the outer one lags somewhat in development. On the second whorl a notch arises on the inner flank of the lobe. At this particular stage, a notch arises in the outer parts of the saddle V/U close to its top, from which a secondary lobe develops.

Comparison

Of the genus *Semenovites* Glazunova (Glazunova 1960) from the sediments of the Upper Albian, characterized by a well-developed first lobe and the complete separation of the third lobe.

(Free translation from original Russian.)

Kopetdagites Iljin, 1975: 157

Type species. *Kopetdagites kopetdagensis* gen. et sp. n. from the sediments of the Upper Cenomanian of Turkmenia.

Diagnosis

Shells high, from compressed to inflated whorl section. Venter is smooth. On early whorls venter is smooth or crenulated, on middle and adult by means of two rows of highly crenulated tubercles, oblique in the side of the flanks and projecting over the ventral sides. The umbilicus is narrow and funnel-shaped. The umbilical tubercles are always high, mammiform. The flanks are covered with sickle-shaped ribs, bifurcating on to the outer half of the flank. On the point of division of the ribs, tubercle-like swellings may arise.

The suture line at a diameter of 40 mm and upwards on the flanks is relatively deep with long side branches and has ventral lobes and up to 9 lobes alternating with the saddles. The first lobe is short, slanted towards the second lobe. The

fourth lobe is small and weakly developed. The fifth lobe is significantly larger than the fourth and somewhat larger than the sixth. The first saddle is always lower than the second. On the inner side are up to six lobes, of which the dorsal is the most prominent. The transformation of the first umbilical lobe takes place by formation, at the beginning, on its exterior and subsequently on the inner side of the notches (branching or dendritic) with their complete separation and transformation into independent lobes later on. On the second whorl, a notch develops in the outer segment of saddle V/U out of which a further secondary lobe develops.

Comparison

Of *Turkmenites* gen. n. characterized by the presence of bifurcating ribs.
(Free translation from original Russian.)

Mediasiceras Iljin, 1975: 159–160

Type species. Mediasiceras beliakovae Iljin gen. et sp. n. from the sediments of the Lower Cenomanian of the south-western spurs of the Ghissarski Range.

Diagnosis

Shells discoidal with high arrow-shaped whorl section, narrow, funnel-shaped umbilicus and tapering to the centre, smooth, narrow, concave on the shells, and ventral side, along the middle of which a low ridge is discernible. The flanks are slightly convex near the middle. Ornament consists of sharp, weak, short-curved ribs on the outer part of the flanks; parts of fine, sickle-shaped striae just begin to appear from the suture and the small tubercles along the edge.

The external suture consists of short, with strongly separated, lateral extensions, ventral lobes, and 8–9 strongly separated lobes, alternating with bifid blunt saddles. The dorsal lobes are peak-shaped.

The distinctly expressed slant of the first lobe (from the ventral lobe) toward the second and the third lobe is a characteristic feature of the suture line of the genus.

Comparison

Of the genus *Proplacenticeras* Spath (1926) characterized by the structure of the suture line, having a distinctly expressed slant of the first lobe towards the second lobe, and an asymmetrical branching base of the second and third lobes. Of the genus *Anaplacenticeras* Iljin (1959) characterized by the presence of a ridge on the ventral side, the presence of umbilical tubercles, a funnel-shaped form of the umbilicus on the shells, and the formation of the suture line, having wider, low saddles and lobes with individual bases, situated on well-defined stems.

(Free translation from original Russian.)

Beschtubeites Iljin, 1975: 162–163

Type species. *Beschtubeites beschtubensis* gen. et sp. n. from the sediments of the Lower Turonian of the lower reaches of the Amudar River.

Diagnosis

Shells high, from compressed to slightly inflated whorl sections. The umbilicus is narrow and funnel-shaped. The venter is smooth and flat, or slightly convex. Umbilical and marginal tubercles are always present in adult specimens. The flanks are covered with sickle-shaped ribs. In places, bifurcation usually produces tubercles or tubercle-like swellings. The suture line of the adult specimens consists of broad, relatively shallow ventral lobes and 8–9 lobes alternating with saddles. The first lobe is parallel or slightly slanted towards the second lobe. The fourth lobe is somewhat smaller, rarely equal to the fifth lobe. The fifth lobe is equal or somewhat larger than the sixth. The first saddle is the highest. The development of the first umbilical lobe results through separation of its four incisions and transformation of them into independent lobes (morphologically first four lobes). In the region of the umbilicus on the second whorl, an umbilical lobe arises which shifts to the external side. The lobes originating in the area of the umbilicus, either undergo double division or remain undivided and shift on to the external or internal side.

Comparison

Of *Kopetdagites* gen. n., is characterized by the structure of the suture line, of which the first lobe at least may have a very slight slant towards the second lobe, but at the same time the base of the lobe is not displaced towards the ventral side and the first saddle is always higher than the second.

(Free translation from original Russian.)

Diplacomoceras Hyatt, 1900 (1903, p. 242)

'This genus resembles *Engonoceras* quite closely in its involute compressed volutions and channelled venter bordered by continuous ridges, and in the tuberculation of the sides it is sufficiently near to be included in that genus if the sutures were unknown. These are, however, well known, thanks to Schlüter's fine figures, and they appear to be similar to those of *Placenticeras*. This genus therefore combines the external characters of *Engonoceratidae* with the sutural lines of *Placenticeratidae*, and perhaps ought to be placed in a separate family.

The young, however, are unknown, and it is perhaps better to wait until their development places their affinities on a firmer basis. It is also possible that they may be accounted for as members of the *Placenticeratidae* that were arrested in their development, retaining the neanic condition of the venter and lateral zones in their later stages, but not arrested in their sutures, which approximate to those of *Placenticeras*.'

Stantonoceras Johnson, 1903: 136

'Shell large in typical species; descended from the same ancestor as *Placenticeras*; having stages of growth corresponding to ancestral types which possessed, in successive generations, keels that were very narrowly flat, channelled, and alternately nodose; but so far advanced at maturity as to bear little or no resemblance to the typical *Placenticeras*; outer whorls broadly rounded or subquadrate in cross-section; moderately embracing; definite ventral keel nearly or quite obsolete; umbilical angle nearly or quite imperceptible; surface ornamented with more or less prominent nodes, elongated nodes or pseudocostae; septa similar to those of *Placenticeras*, but most simple and less crowded.

Although somewhat less accelerated than the type of this genus, I am of the opinion that *Ammonites guadaloupa* Roemer should be included here. It is of course one of the transition types, and its generic reference must be more or less a matter of judgment. But it has advanced so far from the original stock, and has so many features in common with this genus, that it seems to me impossible to classify it elsewhere.'

Proplacenticeras Spath, 1926: 79

'... is of Turonian-Coniacian age and differs in suture-line as well as in whorl shape and ornamentation.'

Pseudoplacenticeras Spath, 1926: 79

'This differs from *Diplacmoceras* Hyatt, by absence of ventral groove, inner row of tubercles, and less compressed young stage.'

Anaplacenticeras Iljin, 1959: 201

Type species. Anaplacenticeras turkmenense sp. nov. from the Cenomanian deposits of Kopet-Dagh.

Diagnosis

Shell flat, with high whorl section, deep, step-like umbilicus. Umbilical wall steep, umbilical edge is sharp. Siphonal side is narrow, slightly concave on the shells and weakly convex in the middle, falcate ribs. On the umbilical edge are infrequent, very small tubercles.

Suture line

The siphonal lobe is weakly developed, very short. The first lobe is deep. The second and third have a common base, are massive and strongly incised. The fourth lobe is short, significantly smaller than the fifth. Saddles are narrow, low. The third saddle, subdividing the second and third lobes, is very small and low.

Comparison

According to the shell form, the formation of the umbilicus and the ornamentation, *Anaplacenticeras* gen. n. suggests the Albian *Cleonicer* *Cleon*

Orb., *Cl. mangyschlakensense* Luppov, but the type of suture line and whorl section of these genera is clearly distinct.

In *Anaplacenticerias* gen. n. the siphonal side is flat as distinct from the pointed or strongly rounded one of the genus *Cleonicerias* Parona & Bonarelli.

The suture line of *Anaplacenticerias* gen. n. has more massive lobes and narrower saddles. In *Cleonicerias* Parona & Bonarelli the ratios are the reverse.

Anaplacenticerias gen. n. is distinguished from the smooth representatives of the genus *Placenticerias* Meek (*Pl. kharesmense* Lah., *Pl. arkhangelskii* Iljin) by a stepped form of umbilicus, very small umbilical tubercles, and a distinct umbilical edge. The last two characteristics connect the genus with the genus *Proplacenticerias* Spath, but the suture lines in these genera are different.

(Free translation from original Russian.)

Gissarites Iljin, 1959: 727

Diagnosis of the genus

Shell discoidal, involute with narrow umbilicus and wedge-shaped whorl section. Maximum width is located at the umbilical edge or on the lower third of the flanks. On internal casts the siphonal side is pointed in the form of a flat keel; in shelly preservation it is compressed, narrow, not expanding with the growth of the whorls and along the edges of it, minute elongated tubercles are located in zig-zag fashion. The flanks are smooth. Along the umbilical edge a series of high tubercles is located. Approximately at mid-flank there are weak bulges. The thickness of the shell differs in different parts of the shell. It reaches maximum thickness in the region of the umbilicus on the umbilical edge, and along the edges of the siphonal side. In consequence of this, the umbilicus is more open in the middle and has steep, high walls, while on the shells the umbilicus is narrower with relatively sloping walls.

The suture line is of the placenticeratid type, and consists of bulb-shaped lobes and divided, rounded saddles. The siphonal lobe is wide, shallow, with short, blunt lateral branches. The lobes on the flanks are well developed. The deepest of them is the third lobe; the sixth lobe is longer and wider than the fifth and only a little less deep than the fourth. The saddles are rounded, and one and a half to two times wider than the lobes. The first saddle is trifid with a significantly developed middle branch. The remaining saddles are bifid.

Comparison

In contrast to the nearest genus, *Placenticerias* (Meek, 1876, p. 462), *Gissarites* gen. nov. has a tapered siphonal side at the centres and is very narrow; the siphonal side on the shells not expanding with the growth of the whorls. The suture line of the new genus is distinguished from the suture line of the genus *Placenticerias* by an inverse ratio of the depth of the fifth and sixth lobes. In the genus *Placenticerias* the fifth lobe is larger than the sixth; in the new genus the sixth lobe is larger than the fifth; the lateral branches of the siphonal lobe are short and blunt in contrast to the paw-shaped ones of *Placenticerias*.

Species composition and distribution

Two species in the genus are known: *Gissarites kysylchense* sp. nov. and *Gissarites tagamense* sp. nov. They occur in the Maastrichtian deposits of the south-western spurs of the Ghissarski Range. In the present article the first of the named species is described, which is taken as the type of genus.

(Free translation from original Russian.)

Parastantonoceras Collignon, 1965b: 17

The generic characters are very close to those of *Stantonoceras* of the Santonian-Campanian: there are two rows of tubercles, one umbilical of strong pointed tubercles, one large, blunt, flat and latero-external disappearing on the body chamber; the external region bears strong, elongate tubercles in two parallel rows and alternating. But here: the umbilical tubercles are at the summit of the umbilical wall, the latero-external tubercles on the second third of the flanks and the tubercles limiting the external region are very strong instead of being small. On the other hand, the suture shows a reduced number of elements, the saddles much larger and, as a result, fewer, widely separated lobes.

(Free translation from the original French.)

Asiatostantonoceras Iljin, 1975: 172

Type species. *Stantonoceras tagamense* Iljin (1959) from the sediments of the Upper Santonian of the south-western spurs of the Ghissarski Range.

Diagnosis

Shell discoidal, with narrow venter, slanting umbilical wall and inflated flanks, along the middle of which a row of tubercles is situated. There is almost no broadening of the venter with development of the shell; its sides are bordered by low, tooth-like tubercles. In the early stages of development there are three rows of tubercles on the flanks—umbilical, upper lateral and marginal. Later, the upper lateral tubercles disappear, but the umbilicals, in proportion to the flattening out of the umbilical wall, shift behind its rim on to the flanks, and occupy a central position on it. The suture line consists of a relatively deep ventral lobe with short lateral branches, and nine lobes alternating with saddles. The first lobe is shorter than the ventral, the fourth is a little larger than the fifth, the fifth is larger than the sixth. The saddles, except the first, are rounded and bifid. The first saddle is the highest, compressed and tapered toward the ventral side and top. To this genus, beside the type species, one must also refer those described from the Upper Santonian of Western Germany, *A. schlüteri* (Schlüter, 1872, pl. 14 (figs 2)), *A. pseudo-orbignyanum* Hyatt (Schlüter 1872, pl. 15 (figs 3–4)), *A. bidorsatum* Müller, [and] Wolleman & Roemer (Müller & Wolleman 1906, pl. 3 (fig. 1), pl. 4 (fig. 5), pl. 9 (fig. 1 only)).

Comparison

Of the genus *Stantonoceras* Johnson, characterized by the form of the whorl section, narrow venters, by strongly developed umbilical tubercles occupying a central position on the flanks and by the disappearance of upper lateral tubercles with growth of the shell.

(Free translation from original Russian.)

Baghiceras Chiplonkar & Ghare, 1976: 3

Type species: Baghiceras ambai sp. nov.

'Diagnosis

Evolute; cross-section broadly elliptical tending to be subcircular to circular; venter broadly rounded with clavi which may be tuberculate; strong spinose umbilical tubercles and strong ventrolateral tubercles joined by different patterns of ribbing; suture somewhat poorly developed placenticeratan type.

Age

Cenomanian–Turonian

Remarks

As compared to other members of the subfamily Baghiceratinae, this genus has less developed suture. It differs from *Placenticerias* (its tumid species) also by having three rows of tubercles and the umbilical ones not migrating outwards. From *Stantonoceras* it differs in having fewer but stronger ventral clavi; while from the genus *Diplacmoceras* it differs in not having pinched ear-like ventral clavi and ventrolateral tubercles. The genus *Hoplitoplacenticerias* differs from the present genus in having typically trapezoidal cross-section and by outward migration of umbilical tubercles.

By its less-developed *Placenticerias* type of suture this genus is much like the more ornamented species of *Knemiceras* (*Knemiceras*), e.g. *Kn. (Kn.) syriacum*, *Kn. (Kn.) attenuatum* and *Kn. (Kn.) gabbi*, and appears to have developed out of *Knemiceras* (*Knemiceras*); and Placenticeratidae is considered to have been derived from Engonoceratidae (Wright, 1957: 390).'

Malwicerias Chiplonkar & Ghare, 1976: 4–5

Type species. Malwicerias variabilis sp. nov.

'Diagnosis

Rather evolute; early whorls essentially compressed tending to broadly elliptical to subcircular to circular cross section; umbilical and ventrolateral tubercles prominent; venter flanked by clavi; ribs weak or absent; suture with few elements.

Age

Cenomanian to Turonian

Remarks

As exemplified by the type species the cross-section varies with stages of shell growth from compressed to circular with venter flattish narrow to broad feebly convex. Suture of typically *Placenticeras* type has few elements as in *Proplacenticeras*.

Fewer but stronger ventral clavi distinguish this genus from *Stantonoceras*. *Hoplitoplacenticeras* by its trapezoidal cross-section clearly differs from this genus. Compared to *Malwiceras* the genus *Diplacmoceras* is distinguishable by its pinched and ear-like clavi and ventrolateral tubercles. Compared to *Baghiceras*, *Malwiceras* has better developed suture, has no ribs and in its cross-section is variable with shell growth from compressed to circular. The genus is named after Malwa, the region in which the Bagh Beds occur.'

Placentoscaphites Chiplonkar & Ghare, 1977: 68–69

'*Genotype. Placentoscaphites dangerfieldi* sp. nov.'

Diagnosis

Shell moderately large with oval umbilicus; whorls more or less compressed to convex and tumid; ornamentation of simple low ribs with or without weak umbilical tubercles and ventral clavi; ventrolateral tubercles if present may tend to be clavate. Suture placenticeratid but distorted.

Age

Cenomanian–Turonian.

Remarks

The polyphyletic origin of uncoiled ammonoids has been realized since long by workers like Smith, Nowak, Spath, Reeside, etc., and Nowak has remarked that 'whether scaphitid forms do not occur in other families and genera may be established by future workers'. The provincial development of these in independent areas is considered by Cobban and Matsumoto as particularly apparent from Turonian onwards.

The generic nomenclature such as *Holcoscaphites* Nowak, *Acanthoscaphites* Nowak, *Hoploscaphites* Nowak and *Desmoscaphites* Reeside, which is already currently used, indicates the close affinities of these heteromorphs to the genera from which they are considered to have been derived.

Association of these heteromorphs with abundantly represented placenticeratids, coupled with their placenticeratid sutural pattern, indicates that these Bagh heteromorphs have placenticeratid affinities. They are placed here, like other heteromorphs, under the admittedly polyphyletic family Scaphitidae, and their

apparently having been derived from placenticeratid stock has led us to name the genus *Placentoscaphites*.'

Sancarlosia Chiplonkar & Ghare, 1978: 79

Type species. *Placenticeras sancarlosense* Hyatt, 1903 (pl. 30 (figs 1-3)).

'Diagnosis

Form tumid; sides feebly convex, venter broad with alternating clavate tubercles; tubercles at shoulder tending to be bullate; umbilical tubercles tending to be bullate and migrating mid-ventrolaterally; suture *Placenticeras*-like with first adventitious saddle in first lateral saddle broader than others.

Age

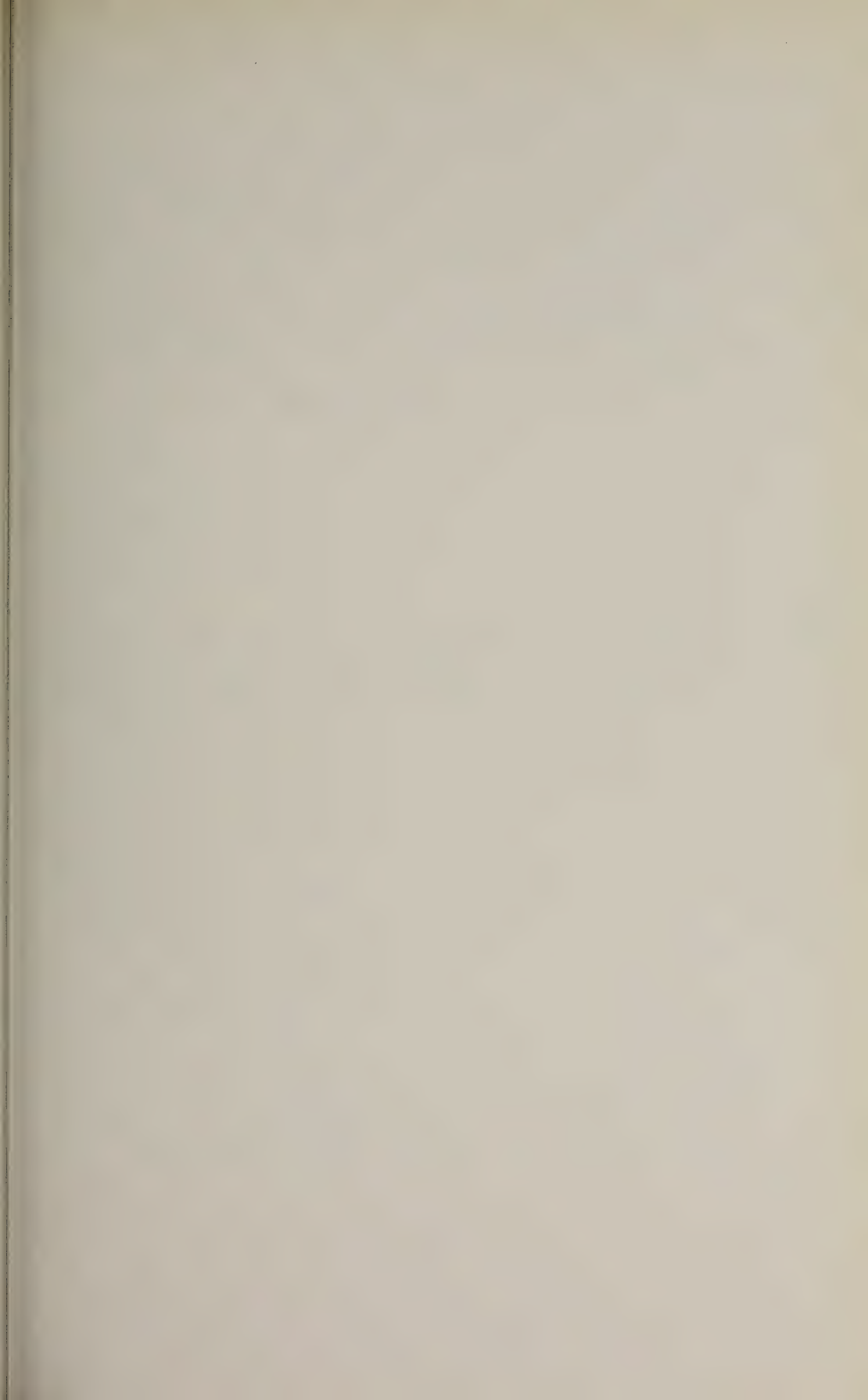
Senonian.

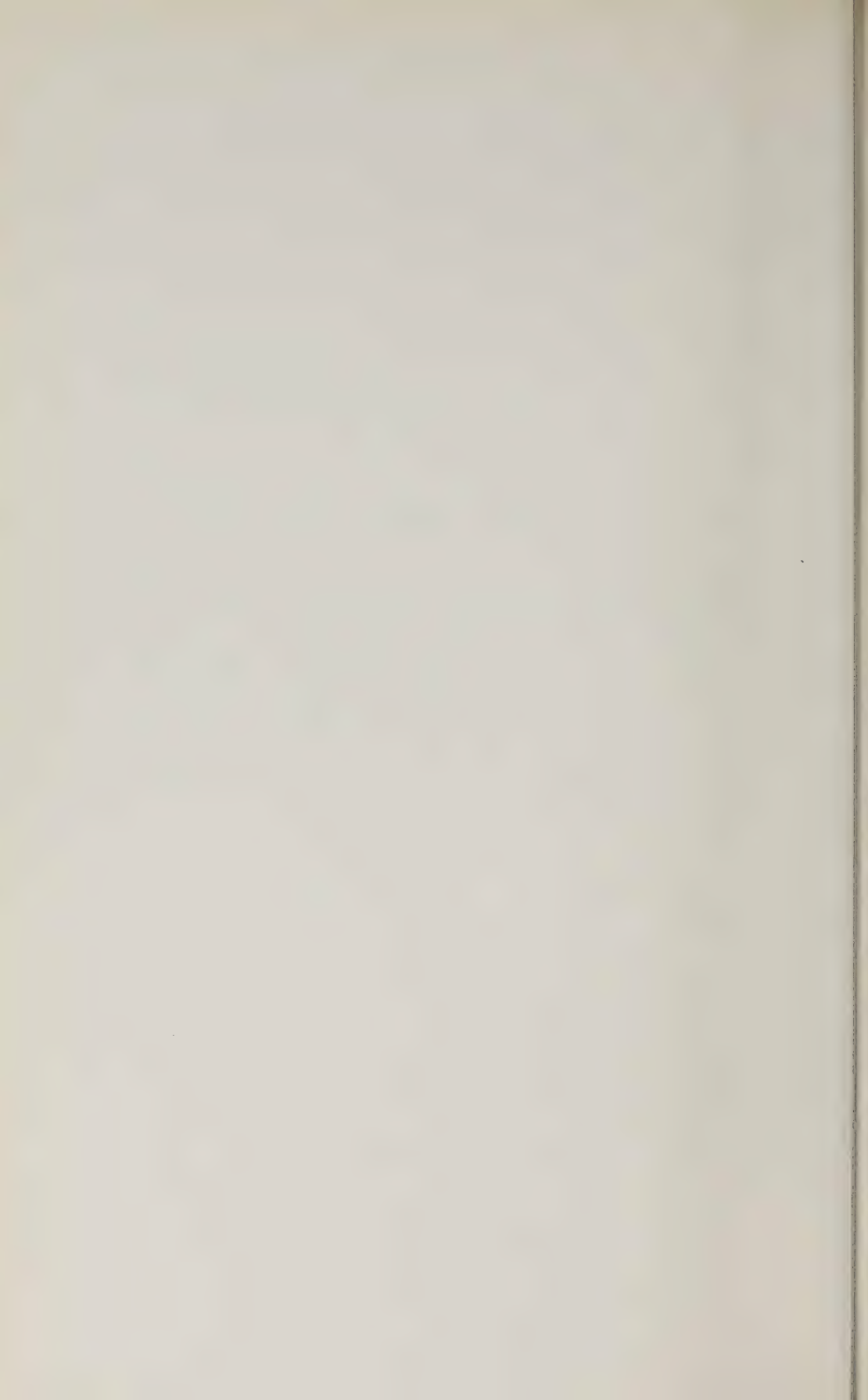
Genus is named after locality of origin, i.e. San Carlos (Mexico).'

NOTE ADDED AT PROOF STAGE

A new genus, *Rapidoplacenticeras* Alabushev, 1988 (type species *Proplacenticeras sutherlandbrowni* McLearn, 1972), has been described from the Upper Albian. It is said to differ from (*Pro-*)*Planticeras* by its lack of ornament, narrow umbilicus and more incised suture line.

ALABUSHEV, A. I. 1988. *Rapidoplacenticeras*—a new genus of Cretaceous ammonoids. *Paleontological journal* **1988** (1): 109–112, 3 figs.





6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers.

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* . . .'; '... in *C. namacolus* (Fig. 10) . . .'
- The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should preferably be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

HERBERT CHRISTIAN KLINGER

&

WILLIAM JAMES KENNEDY

CRETACEOUS FAUNAS FROM ZULULAND
AND NATAL, SOUTH AFRICA.
THE AMMONITE FAMILY
PLACENTICERATIDAE HYATT, 1900;
WITH COMMENTS ON THE
SYSTEMATIC POSITION OF THE GENUS
HYPENGONOCERAS SPATH, 1924

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Note: no comma separating name and year
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FISCHER, P. H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archives de zoologie expérimentale et générale* **74** (33): 627–634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) **2** (17): 309–320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bulletin of the Bingham Oceanographic Collection, Yale University* **17** (4): 1–51.

THEILE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* **4** (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* **16**: 269–270.

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THE PSEUDOCEANIC-OCEANIC INTERFACE

By

P. ALEXANDER HULLEY

&

J. R. E. LUTJEHARMS

Cape Town

Kaapstad

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PART 3.

THE PSEUDOCEANIC-OCEANIC INTERFACE

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(With 8 figures and 7 tables)

[MS accepted 24 February 1989]

ABSTRACT

The distributions of lanternfishes (Myctophidae) from various cruises of the R.S. *Africana* off the west coast of southern Africa were examined in order to elucidate the pseudoceanic-oceanic interface in the eastern South Atlantic. Thirty-six night RMT-8 hauls to 120 m and along nine transect lines across the southern African west-coast continental shelf/slope (25°32'–34°55'S 12°27'–17°35'E) were made during the Phyllosoma Survey in August 1984 (winter). An investigation of cross-shelf/slope zonation is undertaken using lanternfish abundances and the Bray-Curtis similarity measure with group average sorting and multi-dimensional scaling. Two groups of stations are recognized. Their clustering is correlated to bottom depth and their interface is best demarcated by the 800-m isobath. The 'in-shore' group is characterized by the pseudoceanic species *Lampanyctodes hectoris*, whereas 'off-shore' group indicator species include the oceanic, mesopelagic myctophids *Ceratoscopelus warmingii*, *Diaphus hudsoni* and *Diaphus meadi*. Examination of additional data suggests a seasonal, off-shore displacement in the distribution of *Lampanyctodes hectoris*. During the summer upwelling period the species occurs mainly in-shore of the 300 m isobath and its off-shore distributional limit approximates the 500 m bottom contour. In winter its distribution extends to the 1 000 m isobath but it may be taken at lesser densities over depths in excess of 3 000 m. Similar seasonal patterns are not evident for oceanic myctophids, suggesting that water-column depth and the potential to undertake diurnal migration may be the major factor governing the shoreward distribution of these oceanic species. In the southern Benguela region at least, the seasonal difference in the distribution of *Lampanyctodes hectoris* appears to be geared to the effect of frontal dynamics on the availability of food in summer, and to a migration into deeper waters during the winter-spring spawning period.

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INTRODUCTION

The existence of a frontal system close to the shelf break in the southern Benguela region (Bang 1971, 1973a, 1973b; Bang & Andrews 1974), and the association of frontal zones with increased biomass and productivity, have recently given impetus to the study of the physical oceanography of the mixing area seawards of and parallel to the main coastal upwelling core off the west coast of southern Africa (Brundrit 1981; Shannon *et al.* 1983; Van Foreest *et al.* 1984; Shelton *et al.* 1985; Lutjeharms & Meeuwis 1987; Lutjeharms & Stockton 1987). Allied biological research on chlorophyll, copepod and fish distributions have been reviewed by Shannon & Pillar (1986) and Crawford *et al.* (1987), while Shelton (1986) has commented on the significance of the front to fish reproductive strategies. The present paper deals with a preliminary investigation of the biological effects of the interaction between bottom topography and large-scale hydrographic features on the distribution of the predominantly oceanic family Myctophidae in the eastern South Atlantic.

The continental slope not only limits the landward distribution of the oceanic mesopelagic and bathypelagic ichthyofauna (Pearcy 1964; Badcock 1981; Hopkins *et al.* 1981; Merrett 1986; Parin 1986), but also provides an environment for the development of a recognizable and trophically dependent community of benthic and benthopelagic fishes (Parin & Golovan 1976; Marshall & Merrett 1977; Rätz 1984). However, pseudoceanic derivatives of certain fish families, including the Myctophidae, may occupy the region above the upper continental slope and inshore of the continental shelf break (Nafpaktitis & Paxton 1968; Krefft 1970; Kawaguchi & Shimizu 1978; Nafpaktitis 1978; Hulley 1981, 1986b; Bekker 1983; Rubiés 1985; Hulley & Prosch 1987). These derivatives include both obligatory pseudoceanic species and facultative pseudoceanic species, the former often the numerical dominants of the pelagic slope populations (Merrett 1986).

Although *Lampadena pontifex* has been caught sporadically south to 28°30'S and *Diaphus taaningi* south to about 24°S off the west coast of southern Africa (O'Toole 1976; Hulley 1981, 1986a, 1986b; Rubiés 1985; SAM data), and although isolated specimens of *Diaphus garmani* have been recorded at about 34°S in Agulhas Water, only a single, numerically dominant, pseudoceanic, myctophid species, *Lampanyctodes hectoris*, is known from the southern Benguela region (Hulley 1986b; Prosch 1986). The latter species has been fished commercially and has accounted for up to 9.4 per cent (42 400 metric tons) of the total annual pelagic catch by the South African purse-seine fishery (Hulley & Prosch 1987).

Few sampling cruises have been undertaken off the west coast of southern Africa to provide specific data for analyses of the pseudoceanic-oceanic interface, but lanternfish specimens collected in August 1984 during the Phyllosoma Survey (Cruise 023) by the Sea Fisheries Research Institute, Cape Town (SFRI) allow for an investigation of slope-shelf distributional phenomena during their

winter manifestation. However as a *caveat*, it must be pointed out that hydrographic conditions during August 1984 may be atypical of winter, since the period of sampling fell within the second phase of the 1984 Benguela El Niño event (September 1983–January 1984) (Shannon *et al.* 1986). The extended warm cycle apparently continued through to 1986 (Shannon & Agenbag 1987), although the warming in 1984 was followed by substantial cooling between November 1984 and October 1985 (L. V. Shannon, SFRI, pers. comm.).

Myctophid data sets from additional SFRI cruises are also analysed in order to examine the possibility of distributional variability on a seasonal basis. The results represent average, seasonal, large-scale patterning and do not purport to examine the high-frequency variability that characterizes the southern Benguela region, particularly during its summer upwelling phase (Shannon 1985).

MATERIALS AND METHODS

During the 1984-Phyllosoma Survey (SFRI Cruise 023) from 14 August to 24 August, 36 stations, situated on nine transect lines extending across the shelf break (Table 1, Fig. 1), were occupied off the west coast of southern Africa by R.S. *Africana* with an opening-closing RMT-8 net (Baker *et al.* 1973). For each oblique haul, the water temperature was recorded at 5-m depth intervals by a probe housed in the Universal Underwater Unit (U³), which also operated the net-closing mechanism. From this record temperatures were extracted at 10-m depth intervals for depths between 0 m and 40 m, and at 20-m depth intervals for depths between 40 m and 120 m (Table 2). In addition, six CTD casts (Fig. 1: CTD₁–CTD₆) were made to investigate the density structure in the off-shore region and its variation with latitude. Temperature profiles at these stations are given in Figure 2.

Due to malfunction of the jaw mechanism of the U³ device that caused premature (and unpredictable) net closure (Pollock 1984), data from stations 1 (1) through 2 (4) are unreliable and have therefore have not been taken into account in the ensuing analyses; these stations yielded 153 lanternfish specimens comprising nine genera and 15 species. No specimens were caught at station 3 (1) due to gear failure and the haul at station 9 (4) was aborted; these stations are also not included in the analyses.

The location of the main upwelling fronts for the months August 1983 and August 1984 were established by using thermal infra-red images from the radiometer on board the *Meteosat II* satellite. The instrument measured in the 10,5–12,5-m waveband and daily data sets were appropriately contrast-enhanced for this ocean area. The spatial resolution in the area was less than 5 km by 5 km. No atmospheric corrections were made, so that absolute temperatures were not available from the imagery, but temperature profiles for the stations from the August 1984 cruise are given in Table 2. Experience has shown that the main upwelling front is sufficiently distinct so that its identification is

TABLE 1

R.S. *Africana* Cruise 023: Station data. BDepth = bottom depth; Comp. No. = computer generated number; Duration = duration of haul; FDepth = fishing depth; LMT = local mean time (hours:minutes:seconds); Speed = ship's speed.

St. No.	Comp. No.	Position		Date	LMT	Duration (mins)	FDepth (m)	Speed (knots)	BDepth (m)
1 (1)		25°32,18'S	13°33,76'E	15.08.1984	20:18:19	60	120-20	2,60	525
1 (2)		25°33,00'S	13°11,75'E	15.08.1984	23:15:00	60	120-20	2,40	1 561
1 (3)		25°31,91'S	12°49,91'E	16.08.1984	01:56:26	60	120-20	2,50	2 500
1 (4)		25°29,97'S	12°27,21'E	16.08.1984	04:51:44	60	120-20	2,50	3 060
2 (1)		26°39,75'S	13°33,02'E	17.08.1984	06:32:45	60	120- 0	2,80	950
2 (2)		26°40,80'S	13°13,20'E	17.08.1984	03:26:52	60	120- 0	2,00	2 000
2 (3)		26°44,00'S	12°54,00'E	17.08.1984	00:08:00	60	120- 0	2,30	3 399
2 (4)		26°46,00'S	12°39,00'E	16.08.1984	19:44:00	60	120-20	—	3 270
3 (1)		28°05,24'S	14°29,62'E	14.08.1984	20:05:02	60	120-20	2,80	598
3 (2)	1	28°08,00'S	14°07,00'E	14.08.1984	23:12:42	60	120-20	2,80	1 272
3 (3)		28°07,00'S	13°43,00'E	15.08.1984	02:20:58	60	120-20	2,60	1 433
3 (4)	2	28°09,10'S	13°19,35'E	15.08.1984	05:32:47	60	120-20	2,60	1 300
4 (1)	3	28°52,00'S	14°21,00'E	17.08.1984	20:11:00	60	120- 0	2,50	550
4 (2)	4	29°00,00'S	14°00,00'E	17.08.1984	23:09:00	60	120- 0	2,10	1 491
4 (3)		29°05,40'S	13°38,52'E	18.08.1984	02:07:46	60	120- 0	2,50	1 355
4 (4)	5	29°09,75'S	13°15,86'E	18.08.1984	05:00:53	60	120- 0	2,50	2 950
5 (1)	6	30°32,00'S	15°17,00'E	19.08.1984	05:30:00	60	120-20	2,50	352
5 (2)	7	30°37,80'S	14°55,10'E	19.08.1984	03:28:00	60	120-20	2,50	1 300
5 (3)	8	30°42,74'S	14°32,63'E	18.08.1984	22:57:00	60	120-20	2,50	2 200
5 (4)	9	30°48,37'S	14°10,72'E	18.08.1984	20:09:00	60	120-20	2,20	2 570
6 (1)		31°44,00'S	15°48,00'E	20.08.1984	05:20:00	60	120- 0	2,50	742
6 (2)		31°49,00'S	15°30,00'E	20.08.1984	02:30:00	60	120- 0	2,50	1 750
6 (3)	10	31°55,23'S	15°09,46'E	19.08.1984	23:11:00	60	120- 0	2,50	2 470
6 (4)	11	31°59,93'S	14°51,06'E	19.08.1984	20:46:00	60	120- 0	2,50	2 800
7 (1)	12	32°52,00'S	16°53,00'E	21.08.1984	03:55:00	60	120-20	2,50	408
7 (2)		32°59,50'S	16°34,00'E	21.08.1984	01:08:00	60	120-20	2,50	1 500
7 (3)	13	33°05,14'S	16°12,31'E	20.08.1984	22:05:00	60	120-20	2,50	2 540
7 (4)	14	33°12,02'S	15°49,41'E	20.08.1984	19:25:00	60	120-20	2,50	3 150
8 (1)	15	33°33,61'S	17°32,21'E	22.08.1984	20:00:00	60	120-20	2,50	404
8 (2)	16	33°43,89'S	17°11,00'E	22.08.1984	23:04:00	60	120-20	2,50	837
8 (3)	17	33°51,00'S	16°50,00'E	23.08.1984	02:30:00	60	120-20	2,50	2 450
8 (4)	18	34°00,00'S	16°28,00'E	23.08.1984	05:52:00	60	120-20	2,50	3 120
9 (1)	19	34°19,20'S	17°35,30'E	24.08.1984	04:50:00	60	120-20	2,50	760*
9 (2)	20	34°31,50'S	17°16,50'E	24.08.1984	02:08:00	60	120-20	2,50	2 600*
9 (3)	21	34°43,68'S	16°55,00'E	23.08.1984	22:51:00	60	120-20	2,00	3 100*
9 (4)		34°54,95'S	16°36,52'E	23.08.1984	20:08:00	60	120-20	2,80	3 600*

* = bottom depth plotted from Dingle *et al.* (1987).

independent of the enhancement algorithm employed (Shannon *et al.* 1985). Daily images were scrutinized and the locations of the fronts on all days that were sufficiently cloud-free were superimposed (Fig. 3).

In order to examine the possible effects of seasonality on the distribution of lanternfishes in the southern Benguela region, additional myctophid data from

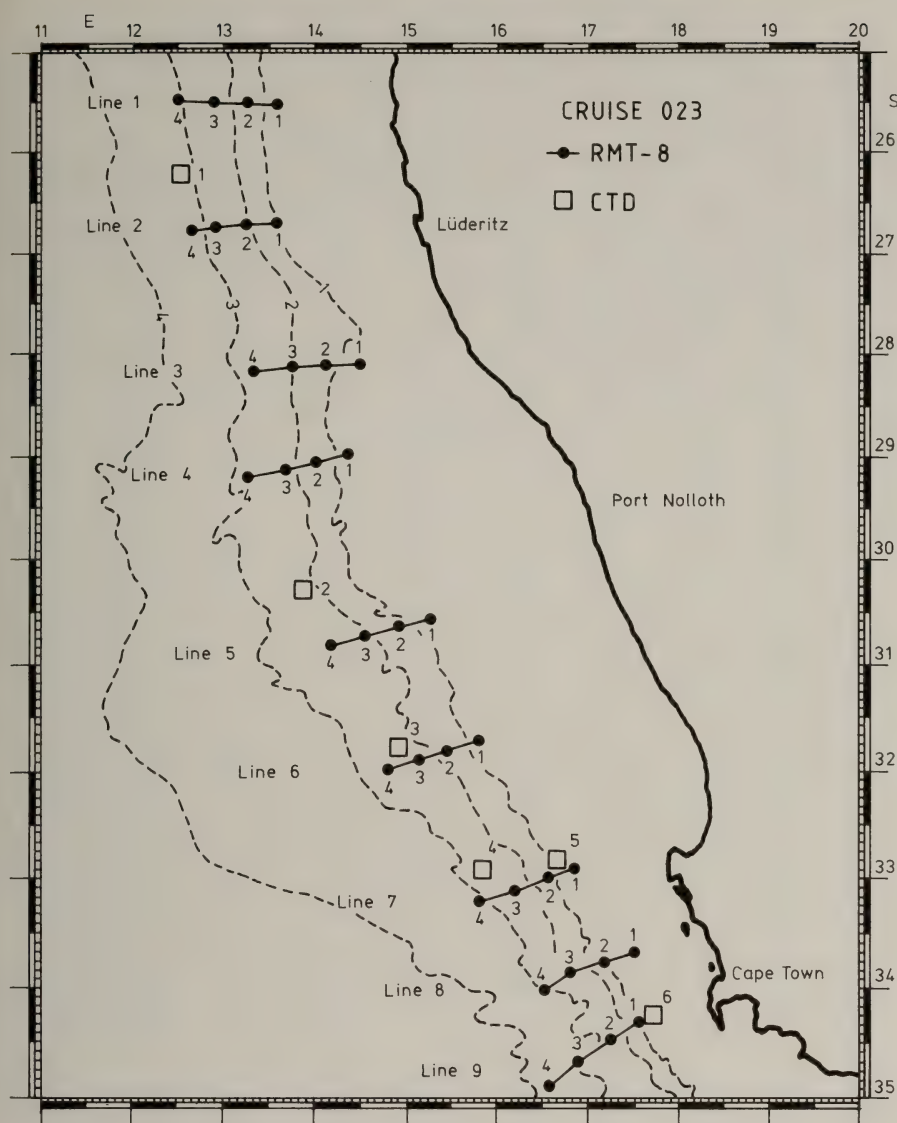


Fig. 1. R.S. *Africana* Cruise 023: August 1984. Station positions. Depth intervals given in metres. 10^3 .

the following SFRI cruises have also been scrutinized: Cruise 002—August 1982: $29^{\circ}12' - 33^{\circ}43'S$, $13^{\circ}04' - 17^{\circ}40,7'E$ (RMT-2); Cruise 009—May 1983: $28^{\circ}38,71' - 34^{\circ}56'S$, $14^{\circ}34,12' - 18^{\circ}19,38'E$ (RMT-8); Cruise 011—August 1983: $29^{\circ}29' - 34^{\circ}56'S$, $14^{\circ}06' - 17^{\circ}35'E$ (RMT-8); Cruise 022—July 1984: $28^{\circ}55' - 35^{\circ}59'S$, $14^{\circ}50' - 19^{\circ}58'E$ (BT-180); Cruise 028—January 1985: $28^{\circ}49' - 36^{\circ}01'S$, $14^{\circ}46' - 19^{\circ}50'E$ (BT-180); Cruise 033—July 1985: $29^{\circ}04' - 36^{\circ}00'S$, $15^{\circ}17,3' -$

TABLE 2

R.S. *Africana* Cruise 023: August 1984. Variation of temperature with depth.

Station No.	Temperature (°C) at depth								
	0 m	10 m	20 m	30 m	40 m	60 m	80 m	100 m	120 m
1 (1)	13,2	13,1	13,2	13,1	13,0	13,0	12,7	12,7	12,2
1 (2)	13,5	13,4	13,4	13,4	13,4	13,3	13,0	12,4	12,2
1 (3)	13,2	13,2	13,2	13,2	12,8	12,5	12,1	11,8	11,5
1 (4)	15,0	15,0	14,9	14,7	14,3	14,1	13,6	13,2	12,3
2 (1)	13,8	13,8	13,8	13,8	13,8	13,6	13,7	13,3	12,3
2 (2)	14,3	14,2	14,3	14,3	14,3	14,4	14,4	14,0	13,2
2 (3)	15,0	15,0	15,0	15,0	15,0	15,0	14,8	14,3	13,9
2 (4)	—	—	—	—	—	—	—	—	—
3 (1)	15,1	15,1	15,1	14,8	14,5	14,1	13,8	12,4	11,0
3 (2)	14,8	15,7	15,7	15,8	15,8	15,8	15,7	15,8	14,2
3 (3)	16,0	16,0	16,0	16,0	16,0	15,8	15,7	15,7	15,0
3 (4)	15,6	15,6	15,6	15,6	15,6	15,6	15,6	15,6	15,0
4 (1)	14,9	14,9	14,9	14,7	14,6	14,2	13,7	13,1	11,4
4 (2)	14,9	14,9	14,8	14,7	14,6	14,4	13,9	13,4	12,3
4 (3)	15,6	15,6	15,6	15,6	15,4	14,8	14,6	14,1	13,6
4 (4)	15,6	15,6	15,6	15,6	15,6	15,6	15,6	15,4	13,5
5 (1)	15,1	15,1	15,0	15,0	15,0	14,9	14,7	14,4	13,8
5 (2)	15,6	15,6	15,5	15,5	15,5	15,5	15,5	15,4	15,2
5 (3)	15,7	15,6	15,4	15,4	15,5	15,4	15,3	15,3	14,9
5 (4)	15,3	15,7	15,7	15,7	15,7	15,6	15,5	15,2	15,1
6 (1)	15,5	15,4	15,2	15,1	15,1	15,0	14,9	14,6	14,0
6 (2)	15,4	15,3	15,2	15,1	15,1	14,9	14,8	14,4	13,7
6 (3)	15,4	15,2	15,2	15,2	15,2	15,2	15,1	14,8	14,1
6 (4)	15,6	15,4	15,3	15,3	15,2	14,9	14,8	14,6	14,2
7 (1)	15,3	15,3	15,2	15,1	15,1	15,1	15,1	15,0	14,4
7 (2)	15,6	15,5	15,3	15,3	15,3	15,1	15,2	15,0	14,6
7 (3)	15,4	15,3	15,2	15,2	15,2	15,2	15,1	14,9	14,9
7 (4)	15,7	15,6	15,5	15,5	15,5	15,3	15,3	15,2	15,2
8 (1)	15,5	15,5	15,4	15,3	15,2	15,4	14,7	13,7	13,3
8 (2)	15,3	15,3	15,2	15,1	15,1	15,1	14,9	15,0	13,9
8 (3)	15,5	15,5	15,5	15,5	15,4	15,3	15,2	15,2	15,0
8 (4)	15,4	15,4	15,4	15,3	15,3	15,2	15,1	15,1	15,0
9 (1)	15,1	15,1	15,1	15,1	15,1	15,1	15,0	15,0	15,0
9 (2)	15,2	15,2	15,2	15,2	15,2	15,1	15,0	14,8	14,3
9 (3)	15,1	15,1	15,1	15,1	15,1	14,9	14,8	14,5	13,6
9 (4)	15,1	15,1	15,1	15,1	14,9	14,6	14,2	12,3	12,0

19°58,5'E (BT-180); Cruise 039—January 1986: 24°28,6'–35°59'S, 13°39,6'–19°53,2'E (BT-180); Cruise 046—July 1986: 28°50'–35°55'S, 14°15,1'–19°49,6'E (BT-180); Cruise 050—January 1987: 28°27,5'–35°44,5'S, 14°15,1'–19°51'E (BT-180); Cruise 054—28°22,1'–36°06,8'S, 14°36,9'–20°00,6'E (BT-180); Cruise 060—March 1988: 32°53,9'–35°09'S, 17°20'–19°29,7'E (BT-180, Engels-308).

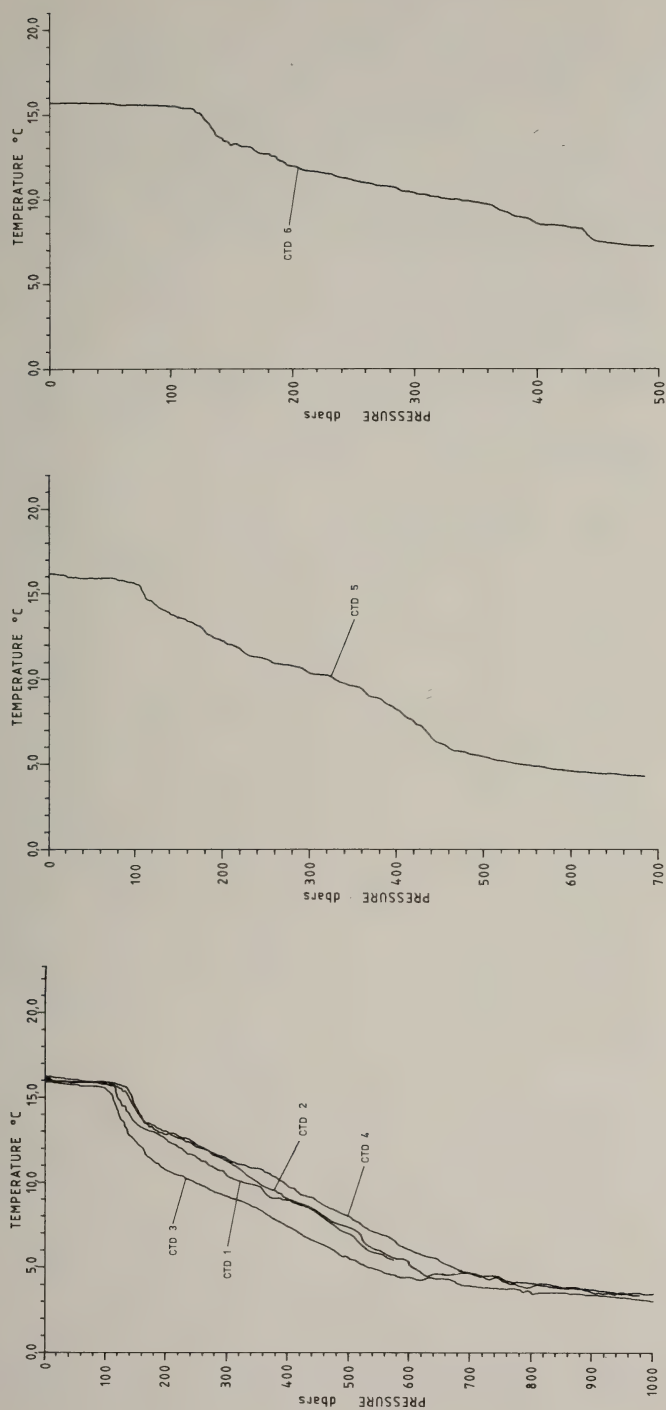


Fig. 2. R.S. *Africana* Cruise 023: August 1984. Temperature profiles from CTD stations. Numbering as in Figure 1.

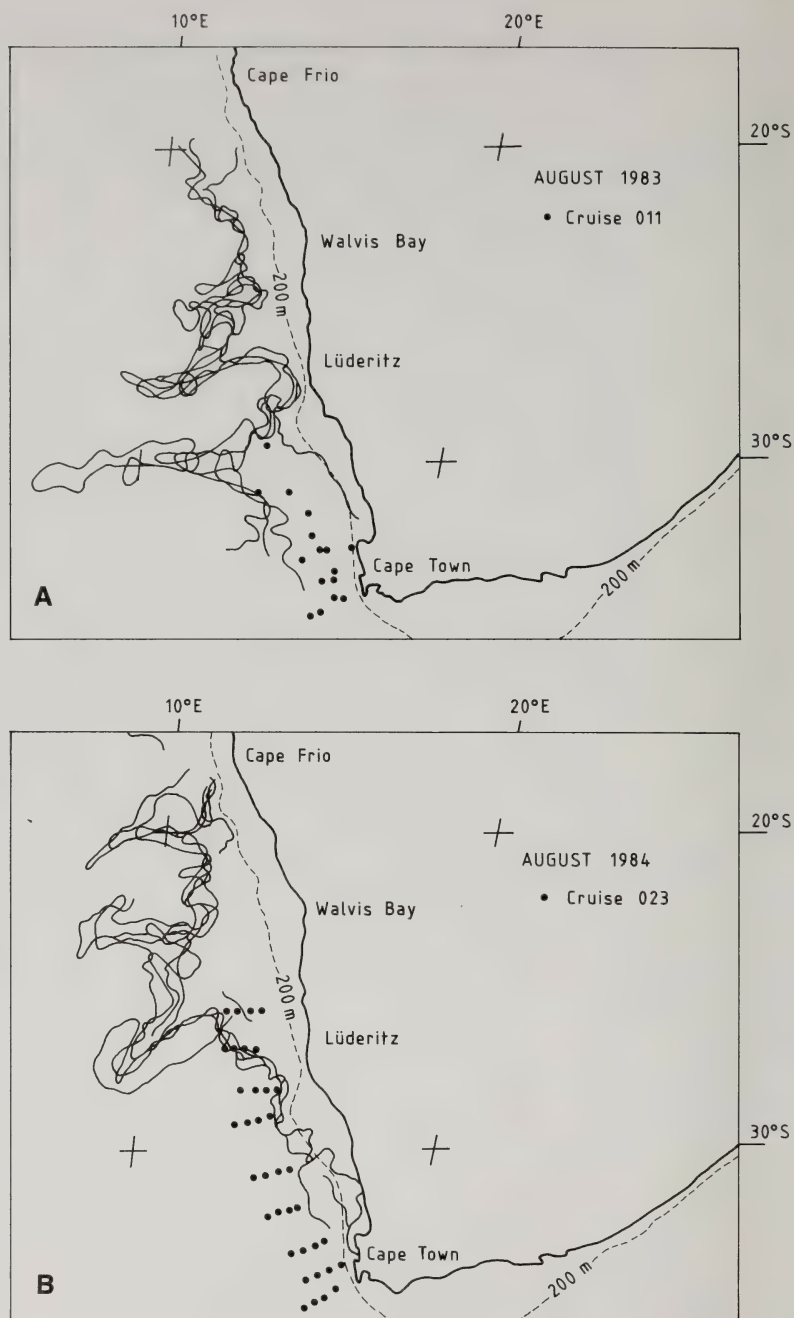


Fig. 3. Montage of locations of the outer limits of cold upwelled water (fronts) as evident in thermal infra-red satellite imagery from *Meteosat II* of the south-east Atlantic in relation to station position for: (A) Cruise 011—August 1983; (B) Cruise 023—August 1984.

RESULTS

The 26 RMT-8 hauls yielded a total of 904 myctophids; the numerical distributions of these are given in Table 3 in relation to the bottom depth of the particular station, and as pseudoceanic or oceanic species in accordance with Hulley (1981). A similar breakdown of the lanternfish data (1 085 specimens) obtained during the SFRI Cruise 011 (Phyllosoma Survey, August 1984) with the identical RMT-8 net and during stratified sampling between 600 m and 0 m, is also given in Table 3.

TABLE 3

Catch rates (specimens.hour⁻¹) for pseudoceanic and oceanic species of Myctophidae from RMT-8 night hauls during SFRI Phyllosoma Surveys in August 1983 and August 1984. No. spp. = number of species.

Bottom depth stratum (m)	PSEUDOCEANIC			OCEANIC	
	No. hauls	No. spp.	Catch rate (specs.h ⁻¹)	No. spp.	Catch rate (specs.h ⁻¹)
AUGUST 1983					
<500	1	1	26,0	3	6,0
500-1 000	2	1	75,0	4	3,5
1 000-2 000	5	1	2,4	29	56,4
2 000-3 000	4	0	0,0	26	109,4
>3 000	1	0	0,0	16	166,0
AUGUST 1984					
<500	3	2	83,7	0	0,0
500-1 000	4	1	20,0	11	13,8
1 000-2 000	8	1	0,4	23	31,1
2 000-3 000	8	1	0,5	20	24,5
>3 000	3	0	0,0	12	22,0
AUGUST 1983 + AUGUST 1984					
<500	4	2	69,3	3	1,5
500-1 000	6	1	38,3	12	10,3
1 000-2 000	13	1	1,2	37	40,8
2 000-3 000	12	1	0,3	32	52,7
>3 000	4	0	0,0	20	58,0

The samples from Cruise 023 resulted in a data matrix of 33 species at 26 stations. The catch rates of myctophids at five of these stations were less than 10 specimens.h⁻¹. Preliminary cluster analysis of the entire data set resulted in the formation of five isolated groups, whose similarity levels were low, i.e. outlier groups, and which tended to obscure the major groupings (*fide* Hulley & Krefft 1985: 43). These five stations were therefore excluded from further analysis. They include: station 3 (3) (4 specimens.h⁻¹); station 4 (3) (2 specimens.h⁻¹); station 6 (1) (3 specimens.h⁻¹); station 6 (2) (6 specimens.h⁻¹); and station 7 (2) (3 specimens.h⁻¹). The reduced data matrix comprised 31 species at 21 stations and was analysed according to the method described by Field *et al.* (1982), and

employed by Hulley & Krefft (1985) for transect analyses of lanternfishes from the 1979-Sargasso Sea Expedition. Standardization of the raw data matrix was unnecessary because the duration of each haul was 60 minutes.

The dendrogram given in Figure 4 shows the station affinities based on root-root transformed abundances of the 31 species included in the reduced data matrix. The broken line drawn at the arbitrary similarity level of 20 per cent delineates two major groups of stations (Group I and Group II). The ordination of the similarity matrix using MDS (Fig. 5) gives the same groupings as the den-

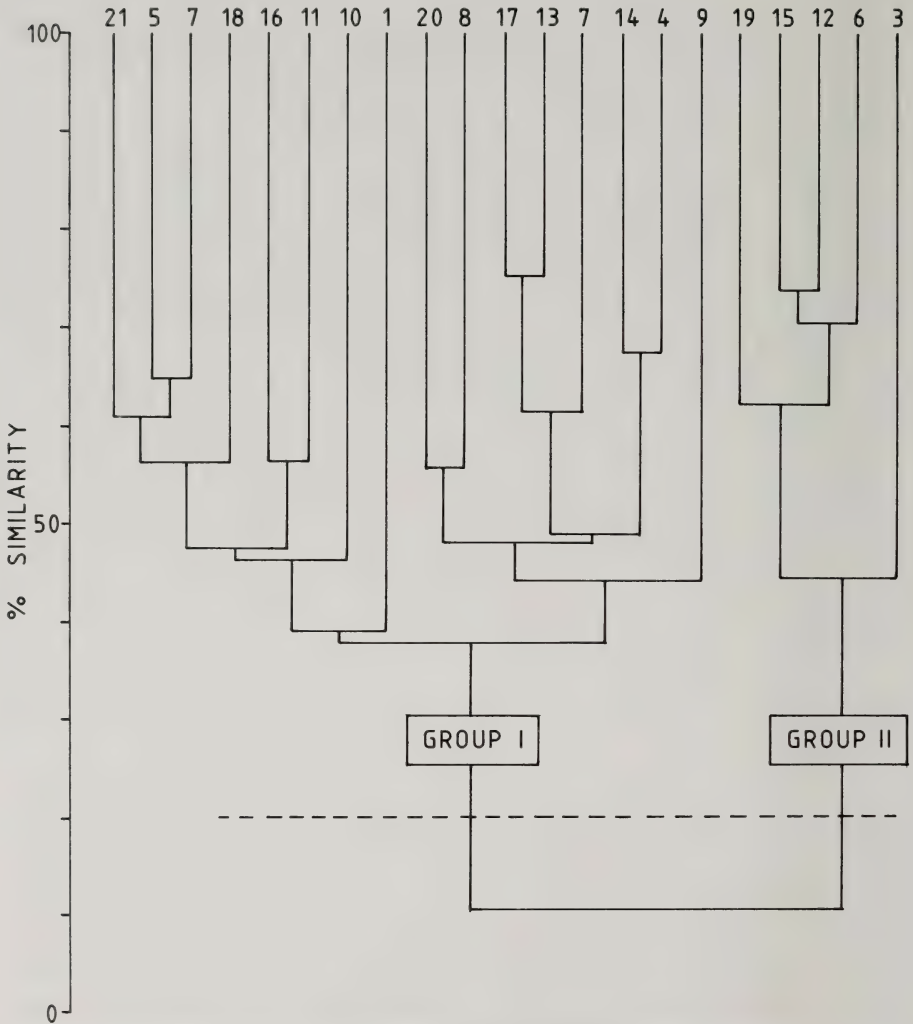


Fig. 4. R.S. *Africana* Cruise 023: August 1984. Dendrogram of station affinities for RMT-8 hauls.

drogram. Although the formation of two subgroups among the Group I stations is indicated at 38 per cent, these groupings are not evident in the ordination and the level of similarity is low when compared to the dichotomy of the Group II stations (44%). MDS-ordination (Fig. 5) supports this contention and suggests that clustering within the Group I stations is ambiguous. Consequently the further classification of the data sets was not undertaken. It should be noted that levels of similarity in the dendrogram are generally low and are the result of the large number of zeros for the less-common species of the matrix.

Results of information statistic (I -) tests for Groups I and II, which are calculated from the numbers of specimens, are presented in Table 4. While $2\Delta I_i$ values should only be employed as a rule of thumb for cut-off limits (Field *et al.* 1982), the data in Table 4 indicates two perfect indicator species for Group I, namely *Diaphus hudsoni* and *Diaphus meadi*. In addition, high $2\Delta I_i$ values for *Lampanyctodes hectoris* (826,880) and *Ceratoscopelus warmingii* (77,732) confirm their identities as Group II- and Group I-indicator species, respectively. As in the classification and ordination procedures, ambiguous results were obtained for the suggested subgroups within Group I. Relatively low values for $2\Delta I_i$ (maximum 15,249) were obtained in comparison to those in Table 4 and to those from the Sargasso Sea analyses (maximum 25 026,911) presented by Hulley & Krefft (1981, tables 4-6, 9-11).

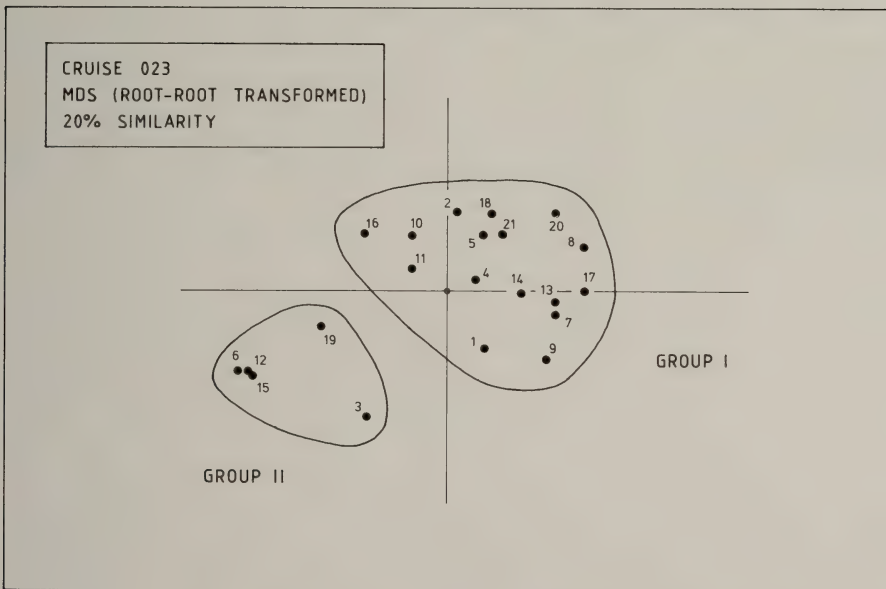


Fig. 5. R.S. *Africana* Cruise 023: August 1984. MDS-ordination of station affinities for RMT-8 hauls.

TABLE 4

R.S. *Africana* Cruise 023: August 1984. Frequencies of occurrence (F) and numbers of individuals (N) of species, ranked according to information statistics, which distinguish Group I (F₁, N₁) from Group II (F₂, N₂). $2\Delta I_i$ values calculated from numbers of specimens. Species above horizontal dotted line have $2\Delta I_i > 6,63$; those below line have $2\Delta I_i > 3,84$; species with $2\Delta I_i < 3,84$ are not included. Maximum values for F₁ and F₂ are given in parentheses.

	F ₁ (16)	N ₁	F ₂ (5)	N ₂	$2\Delta I_i$
<i>Lampanyctodes hectoris</i>	4	13	5	324	826,880
<i>Diaphus meadi</i>	15	236	0	0	128,353
<i>Ceratoscopelus warmingii</i>	15	160	1	1	77,732
<i>Diaphus hudsoni</i>	10	30	0	0	16,316
<i>Lobianchia dofleini</i>	6	11	0	0	5,983
<i>Lampanyctus lepidolichnus</i>	5	19	1	1	5,263
<i>Lampanyctus alatus</i>	4	9	0	0	4,895
<i>Lampanyctus pusillus</i>	4	8	0	0	4,351
<i>Notoscopelus resplendens</i>	5	8	0	0	4,351

DISCUSSION

Since all hauls from Cruise 023 were of 60 minutes duration, were hauled in a uniform manner (D. E. Pollock, SFRI, pers. comm.) and were all fished obliquely at night between 120–0 m or 120–20 m at towing speeds between 2,0 knots and 2,8 knots, and since chemical and productivity measurements were not taken during the cruise, bottom depth and temperature data are the only variables that can be correlated to the station clustering. Temperature data sets at selected depths superimposed on the MDS-ordination indicate little correlation with the station groupings. Examination of the CTD traces (Fig. 2) reveals that the RMT–8 oblique hauls were sampling the upper mixed layer of the water column at all stations and that the lower limits for the mixed layer (top of the thermocline) were similar for casts from both inshore (CTD₅ = 108 m; CTD₆ = 122 m) and offshore (CTD₁ = 132 m; CTD₂ = 120 m; CTD₃ = 108 m; CTD₄ = 138 m) of the 1 000-m isobath.

A better correlation results from the superimposition of the bottom depth data on the MDS-ordination. The initial delimitation of three bottom depth strata demonstrates a gradation from quadrant to quadrant, with shallowest depths in the Group II stations and with depth strata > 1 000 m confined to the Group I stations. The close proximity of station 8 (2) (bottom depth 837 m) of Group I to station 9 (1) (bottom depth 760 m) of Group II should be noted. This suggests that the change in faunal composition lies at some intermediate depth. The correlation of the groupings to the 800-m isobath (Fig. 6) yields the best result, with Group I stations fished over bottom depths in excess of 800 m and Group II stations over bottom depth less than 800 m. Geographic plots of Group I and Group II stations are given in Figure 7. Indicator species for the groupings reinforce these findings. Group I indicator species (*Ceratoscopelus*

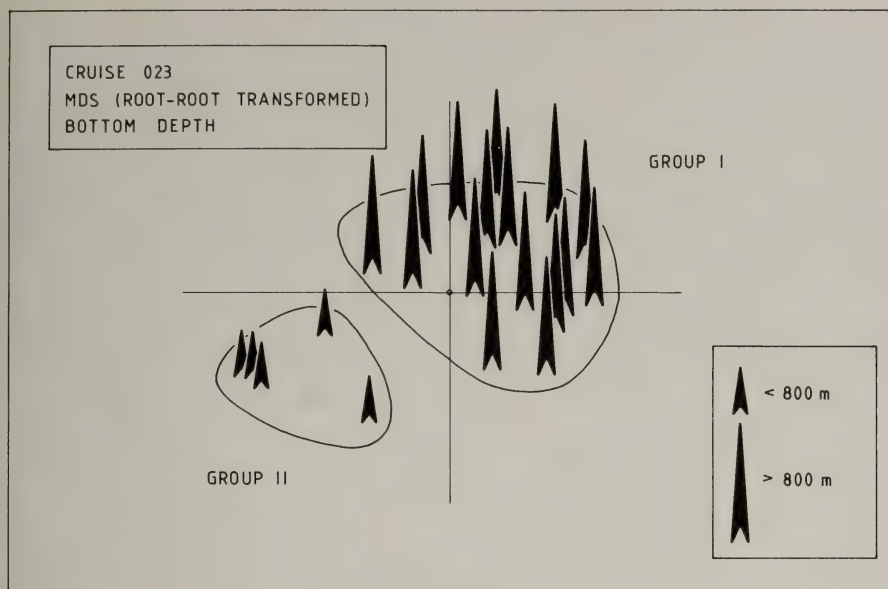


Fig. 6. R.S. *Africana* Cruise 023: August 1984. Bottom depth data superimposed on MDS-ordination for RMT-8 hauls.

warmingii, *Diaphus hudsoni*, *Diaphus meadi*) are oceanic species, whereas the sole indicator species for Group II (*Lampanyctodes hectoris*) is a pseudo-oceanic species characteristic of the shelf area of the southern Benguela region (Hulley 1981, 1986a, 1986b; Hulley & Prosch 1987).

Therefore the landward distribution of oceanic mesopelagic myctophid species and the seaward distribution of pseudo-oceanic myctophid species in the central and southern Benguela regions (28°S–35°S) would appear to be governed mainly by the depth of the water column, with the major faunal change demarcated by the 800 m bottom contour. Across the west Florida continental slope, Hopkins *et al.* (1981, fig. 2) have indicated that the greatest decline in oceanic species occurred where bottom depths shallowed from 500 m to 275 m. Over the Oregon slope off Newport, Percy (1964) has observed this decline where bottom depths shoaled from about 1 000 m and has related this to an inability by mesopelagic fishes to complete vertical migration cycles as the bottom shallows, and the effects of shallow depths on vertical temperature structure and the photo-environment.

Examination of the RMT-8 myctophid data from the 1984-Phyllosoma Survey (Table 3) reveals that catch rates for the two pseudo-oceanic species, *Lampanyctodes hectoris* and *Diaphus garmani*, declined evenly from 83.7 specimens.h⁻¹ over the <500-m bottom depth stratum to 20.0 specimens.h⁻¹ over 501–1 000 m, and dropped abruptly to 0.4–0.5 specimens.h⁻¹ over the 1 000–2 000-m and 2 000–3 000-m bottom depth strata. The species were absent from

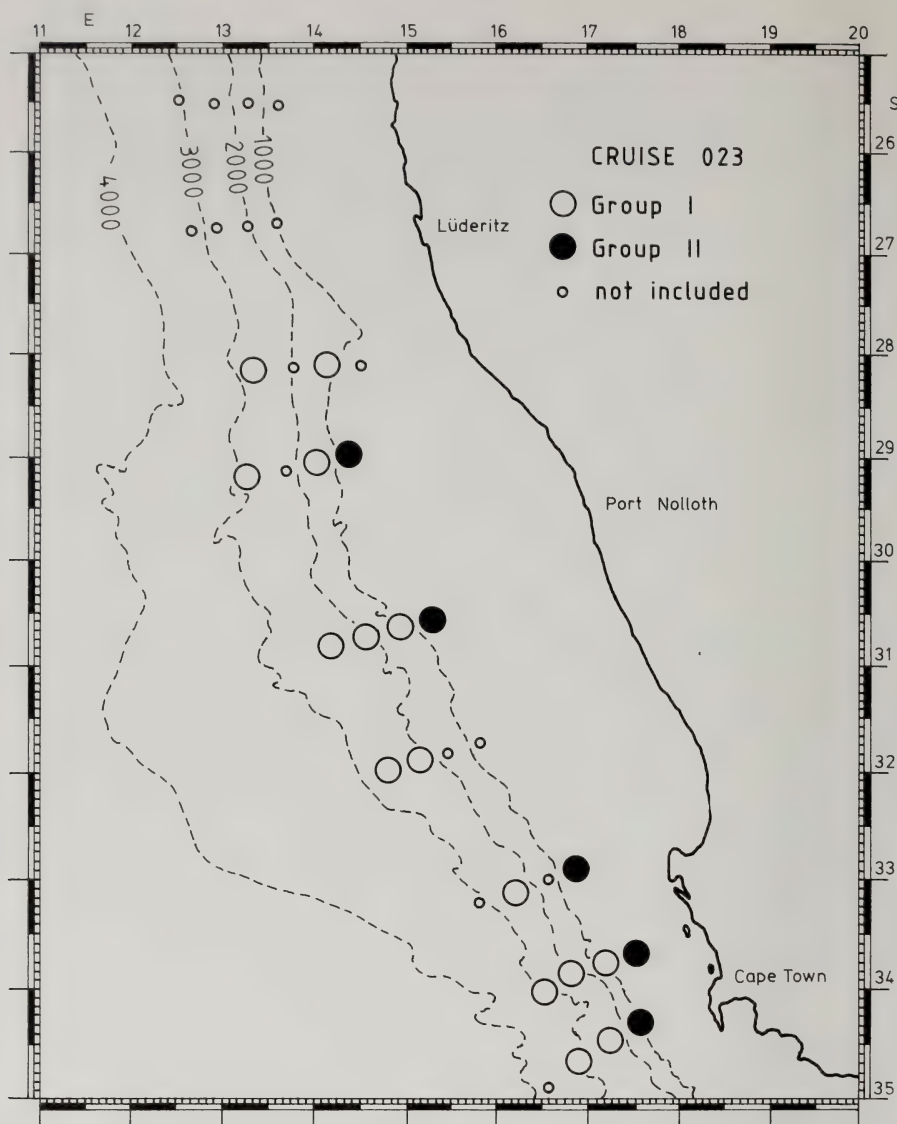


Fig. 7. R.S. *Africana* Cruise 023: August 1984. Geographic plots of RMT-8 hauls showing distribution of Group I and Group II.

the water column where bottom depths exceeded 3 000 m. In contrast, oceanic myctophid catch rates were more-or-less constant (22,0–31,1 specimens.h⁻¹) over bottom depths in excess of 1 000 m and declined to 13,8 specimens.h⁻¹ over 501–1 000 m. Oceanic species were absent where the depth of the water column was less than 500 m. A comparative data subset (13 night hauls) from the 1983-Phyllosoma Survey, during which myctophids were taken in discrete hauls fished

in the upper 250 m of the water column, is presented in Table 3. Here catch rates for the pseudoceanic species, *Lampanyctodes hectoris*, declined from 26,0–75,0 specimens.h⁻¹ at depths shallower than 1 000 m to 2,4 specimens.h⁻¹ over the 1 000–2 000-m depth stratum, and the species was absent over the 2 000–3 000-m and >3 000-m depth strata. In contrast, catch rates for oceanic myctophid species declined evenly shorewards from a value of 166,0 specimens.h⁻¹ (>3 000 m) to 56,4 specimens.h⁻¹ (1 000–2 000 m) and decreased abruptly over depths shallower than 1 000 m.

Pooled data sets from both cruises (Table 3) allow for a more comprehensive examination of the oceanic species spectrum at shallower depths. Whereas a few specimens of three oceanic species (*Diaphus diadematus*, *D. hudsoni*, *Lampanyctus alatus*) were taken over bottom depths shallower than 500 m, 12 myctophid species were taken over depths of 500–1 000 m. The latter include *Ceratoscopelus warmingii*, *Diaphus diadematus*, *D. hudsoni*, *D. meadi*, *D. molis*, *D. perspicillatus*, *Hygophum hygomii*, *Lampanyctus achirus*, *L. australis*, *L. lepidolichnus*, *Notoscopelus resplendens*, and *Symbolophorus boops*. Oceanic species diversity increased from six species inshore of the 1 000-m isobath to 13 species over bottom depths greater than 1 000 m.

Similar trends in the pseudoceanic–oceanic faunal replacement were evident in the myctophid data from BT–180' hauls undertaken during the July 1984–January 1986 SFRI Hake Surveys (Hulley & Prosch 1987, table 2). During this period, oceanic species were never taken over bottom depths less than 301–400 m: shallowest bottom depth 378 m (*Symbolophorus boops*) during the winter cruises; shallowest bottom depth 354 m (*Scopelopsis multipunctatus*) during the summer cruises. On the other hand, *Lampanyctodes hectoris* was taken over bottom depths greater than 500 m in July 1984 and July 1985, and was confined to hauls fished shallower than the 401–500 m depth range in January 1985 and January 1986. While this suggests the possibility of a seasonal shift in the position of the outer boundary limit for *Lampanyctodes hectoris*, these data should be regarded with reservation. It must be noted that: (1) although Roel (1986: 578) has suggested that the presence/absence of *Lampanyctodes hectoris* in BT–180' hauls is 'representative', this gear may not sample the species efficiently; (2) few stations were occupied at depths greater than 500 m during the Hake Surveys; and (3) in contrast to the grouped data sets, absolute maximum values for this species during these cruises, and in three subsequent cruises, were similar: Cruise 022 (July 1984)—515 m (St. A 1563); Cruise 033 (July 1985)—502 m (St. A 2756); Cruise 039 (July 1986)—456 m (St. A 4307); Cruise 054 (July 1987)—460 m (St. A 5899); Cruise 028 (January 1985)—488 m (St. A 2273); Cruise 039 (January 1986)—456 m (St. A 3348); Cruise 054 (January 1987)—467 m (St. A 5306).

However, unpublished data from R.S. *Africana* Cruise 060 off the southwest Cape coast in March 1988 provide additional evidence for the seasonal shift in the distribution of *Lampanyctodes hectoris*. Catch statistics for this species from two daylight and two night lines of stations, which were run in both the

Cape Canyon (SW Cape Columbine) and the Cape Point Canyon (SW Cape Point) regions, are given in Table 5. For this same cruise, catch statistics for five midwater Engels-308 hauls on acoustically identified targets are also given in Table 5. Firstly, these data indicate that the BT-180' net does not effectively sample *Lampanyctodes hectoris*: catch rates with this gear in the 300-m and 500-m bottom depth spectra averaged $0,23 \text{ kg.h}^{-1}$ and $0,003 \text{ kg.h}^{-1}$ respectively, whereas catch rates at similar bottom depths with the Engels-308 net were $66,40 \text{ kg.h}^{-1}$ and $0,36 \text{ kg.h}^{-1}$ respectively. Targeted water-column hauls with the Engels-308 were $15,20 \text{ kg.h}^{-1}$ over 300 m, and $0,01 \text{ kg.h}^{-1}$ over 500 m. In addition, the frequencies of occurrence of *Lampanyctodes hectoris* in BT-180' hauls from the 300 m and 500 m depth spectra was 66,7 per cent and 12,5 per cent respectively, whereas the frequencies in the epibenthic hauls were 100,0 per cent at identical bottom depth strata. Secondly, and from all three sampling strategies, it can be seen that catch rates for *Lampanyctodes hectoris* fall markedly from the 300-m to the 500-m bottom depth strata, and that the species was absent from all stations in the 700-m and 900-m bottom depth strata. The maximum depth of occurrence for the species during Cruise 060 was 552 m (St. A 6986). *Lampanyctodes hectoris* therefore appears to be confined to depths less than about 500 m in summer and is distributed mainly inshore of the 300-m isobath.

Winter catch rates for *Lampanyctodes hectoris* in relation to bottom depth during Cruises 011 and 023 have been discussed above. Pooled data for both

TABLE 5

Catch rates (kilograms.hour⁻¹) for pseudoceanic and oceanic species of Myctophidae from benthic stations (BT-180), epibenthic stations (Engels-308) and pelagic stations (Engels-308) during R.S. *Africana* Cruise 060 (March 1988). SD = standard deviation.

Station type	Bottom depth stratum (m)	No. hauls	Pseudoceanic catch rate (kg.h ⁻¹)		Oceanic catch rate (kg.h ⁻¹)	
			Mean	SD	Mean	SD
Benthic	300	5	0,23	0,27	0,00	0,00
	500	8	0,003	0,01	0,01	0,02
	700	8	0,00	0,00	0,03	0,05
	900	7	0,00	0,00	0,18	0,26
Epibenthic	300	5	66,40	40,92	0,004	0,01
	500	7	0,36	0,74	8,73	5,75
	700	7	0,00	0,00	6,68	6,89
	900	8	0,00	0,00	3,22	1,40
Pelagic	300	1	15,20	—	0,00	—
	500	2	0,01	0,01	5,87	8,30
	700	1	0,00	—	2,78	—
	900	1	0,00	—	232,87	—

cruises (Table 3) indicate a decrease in catch rates from 69,3 specimens.h⁻¹ over bottom depths less than 501 m to 38,3 specimens.h⁻¹ over 500–1 000 m and a marked decline to 1,2 specimens.h⁻¹ and 0,3 specimens.h⁻¹ over bottom depth ranges of 1 000–2 000 m and 2 000–3 000 m respectively. Although the species was not taken over bottom depths greater than 3 000 m during these cruises, three specimens were captured with an RMT-2 over 3 816 m (St. A 002023) during the Phyllosoma Cruise in August 1982. Table 6 summarizes data for the maximum depth of the water column for pelagic captures of *Lampanyctodes hectoris* during the autumn–winter period. These data therefore suggest that *Lampanyctodes hectoris* is more widely distributed in autumn–winter than in summer, being regularly taken to the 1 000-m isobath and less frequently to the 3 000-m isobath. An hypothesis to discuss this seasonality in distribution is advanced below.

TABLE 6

Maximum depth of water column for pelagic capture of *Lampanyctodes hectoris* during the 1982 Phyllosoma Survey (Cruise 002), 1983 Phyllosoma Survey (Cruise 011), 1984 Phyllosoma Survey (Cruise 023) and 1983 Anchovy Acoustic Survey (Cruise 009) by SFRI. BDepth = bottom depth; FDepth = fishing depth; No. specs = number of specimens.

Month	Cruise	Gear	Station No.	FDepth (m)	BDepth (m)	No. specs
May	009	RMT-8	72-05	100-50	2 090	10
August	002	RMT-2	002023	75-0	3 816	3
August	011	RMT-8	P 001	100-25	1 030	12
August	023	RMT-8	6 (4)	120-0	2 800	3

In the Mauritanian Upwelling Region and in summer, Badcock (1981) has recognized both an on-slope and an off-slope myctophid fauna, and a third fauna comprising the obligatory pseudoceanic species *Diaphus taaningi* and facultative pseudoceanic species *Diaphus dumerilii* confined to the shelf-break zone. He has stated (1981: 1489) that 'it is naïve to assume that water column depth has much influence as a separating boundary' and has suggested that shelf–slope zonation is the dynamic response of each group to hydrographic and circulatory characters that maintains core abundances as separate entities, in much the same manner as been shown by Petersen *et al.* (1979) in zooplankton studies off the Oregon coast. The latter authors have proposed that copepod distributions are maintained by two-cell, zonal circulation patterns during active upwelling, and that the seaward limit of nearshore populations is dictated by the dynamics of the upwelling front and its associated longshore current. Larval fish assemblages off Oregon parallel these findings (Richardson & Pearcy 1977; Richardson *et al.* 1980). Prograde shelf-break fronts that are characteristic of eastern boundary current upwelling systems, form a boundary zone to the plankton-rich shelf waters and Owen (1981) has suggested that periodic relaxation or breaching of the front may be biologically important, since they allow for the release of nutrients and plankton into off-shore waters. Frontal relaxation occurs with cessation

of upwelling, which may be either seasonal or episodic depending on the wind regime, whereas the causes of breaching probably involve meanders and eddies, which may be produced by local instabilities of the frontal currents, by outside eddy impingement, or by wave interactions with the front. Such perturbations on the Benguela front, leading to the formation and cross-frontal motion of mesoscale eddies, have been documented from satellite remote sensing (Lutjeharms 1981). Johnson & Van der Spoel (1986) have postulated that the main determinant in the distribution patterns of pelagic species is the food supply, tempered by seasonality. Hulley & Krefft (1985) have examined the distribution of the myctophid *Electrona risso* in relation to the 10 °C- and 15 °C-isotherms at 200 m, and to primary productivity values (50 gCm⁻²y⁻¹ isoline), whereas Yentsch & Garside (1986) have produced a semi-empirical model of two phytoplankton fronts that correspond to the northern and southern limits of myctophid populations in the biogeographic region of the subtropical North Atlantic Ocean.

It is hypothesized therefore that the seasonal differences in the seaward extent of the distribution of *Lampanyctodes hectoris* in the southern Benguela region is causally related to the seasonal dynamic of the frontal system and its associated jet current, and is geared to the biological prerequisites of both the summer feeding phase and winter spawning phase of the species (Hulley & Prosch 1987). Whereas Andrews & Hutchings (1980) have suggested that the influence of the Cape Peninsula upwelling plume expands in summer, seasonal changes inferred from large-scale temporal and spatial averaging of sea-surface temperature data suggest that the events are dominated by summer warming and winter cooling of the sea-surface temperatures within the southern Benguela region (Wooster 1973; Christensen 1980; Parrish *et al.* 1983; McLain *et al.* 1985; Kamstra 1985; Shelton *et al.* 1985). On the basis of data collected over the CELP Survey grid at monthly intervals, Shelton (1986) has stated that the most noticeable feature of the region, and indeed of the whole Benguela System, is the contraction of the area occupied by cool water in summer and the expansion of this zone in winter, and that the influence of upwelling is modulated or squeezed by off-shore warming from late spring to early winter. Shannon (1986: 10) has stated that the Benguela upwelling region is 'pinched' during summer and early autumn between the warm Angola and Agulhas Current systems. Averaged and smoothed sea-surface temperatures over a 50-year period reiterate this seasonality (Kamstra 1985, fig. 6). The seasonal effect is also graphically demonstrated in Gorshkov's (1978) oceanographic atlas at depths of 0 m, 25 m and 50 m; however, the presentations should be regarded with reservation, since the atlas does not show the data distribution on which the figures are based. At the sea surface at least, interannual changes in gross upwelling may be similar to seasonal changes, and can be related to large-scale interannual variability in the environment in the south-east Atlantic (L. V. Shannon, SFRI, pers. comm.).

In summer, off-shore warming together with strong upwelling in-shore, the penetration of Agulhas Bank water, and a steep shelf break close to the coast, combine to cause the formation of an exceptionally strong thermal front and an

associated equatorward, shelf-edge jet current. Both features approximately track the 230-m isobath and truncate the seaward expansion of the in-shore, upwelled water (Bang 1973a; Harris & Shannon 1979; Shelton & Hutchings 1982; Nelson & Polito 1987). The baroclinic jet, which is thought to persist throughout the summer after its initiation in spring (Andrews & Hutchings 1980; Brundrit 1981), appears to extend upwards from the shelf edge (250 m) towards the surface, where some modification occurs under the direct action of wind (Bang 1973a; Nelson & Polito 1987, fig. 3). Plots of the relative abundances of *Lampanyctodes hectoris* in Engels–308 epibenthic and pelagic hauls from Cruise 060 (Fig. 8A) suggest little correlation with temperature, although abundance values greater than 10 kg.h^{-1} tend to be found in-shore of 394-m isobath and at sea-surface temperatures less than 16.4°C . According to the definitions proposed by Andrews & Hutchings (1980) this temperature regime is suggestive of 'mixed water'.

Warm oceanic water close to the coast during the upwelling season also reduces the extent of the productive area and there is good agreement between the positions of the thermal front (15°C – 18°C) and the chlorophyll (colour) front (0.3 mg.m^{-3}) (Shannon *et al.* 1983, 1985; Shelton *et al.* 1985). Elevated plankton standing stocks and microplankton concentrations tend to be restricted in-shore of the front (Shelton 1986). During this season, *Lampanyctodes hectoris* mirrors this distribution and occurs mainly in-shore of the 300-m isobath. Furthermore, its biology is geared to feeding (mainly copepods (61.6%), amphipods (26.6%), euphausiids (11.6%)—Centurier-Harris (unpublished data) *in* Prosch 1986) and to the production of a lipid energy reserve for later use in the winter–spring spawning cycle (Hulley & Prosch 1987). Although ecological investigations of the feeding of *Lampanyctodes hectoris* in the southern Benguela region have not yet been undertaken, Young & Blaber (1986) have demonstrated that the feeding intensity of the species off the Tasmanian coast is greatest during the summer period. The data in Table 5 suggest that there is some 'leakage' of the species to the 500-m isobath, but the causes for a distinct off-shore distributional limit at this depth in summer are not apparent since upwelling filaments (and presumably their plankton content) may extend to the 2 000-m isobath (Lutjeharms & Stockton 1987). Leakage of the species across the 300-m isobath may be linked to the generation of cool-water eddies at the front (cf. *Centropages brachiatus*—De Decker 1984) or to the sinking of plankton-rich surface water along the front (Clowes 1954; Bang 1973a; Andrews 1974; Andrews & Hutchings 1980; Shannon *et al.* 1983; Pillar 1986). Whereas the chlorophyll colour front is well demarcated off the west coast of southern Africa (Shannon *et al.* 1985), chlorophyll does not appear to be concentrated at the front (Shannon & Field 1985, fig. 2—approximate chlorophyll concentrations $<0.1 \text{ mg.m}^{-3}$ west of front; $2\text{--}3 \text{ mg.m}^{-3}$ in the frontal zone; and $3\text{--}9 \text{ mg.m}^{-3}$ inshore of the front) and Hutchings (1981) has found no particular association of higher zooplankton biomass with the frontal zone. However, pronounced peaks of mesozooplankton do occur immediately inshore of the front after periods of

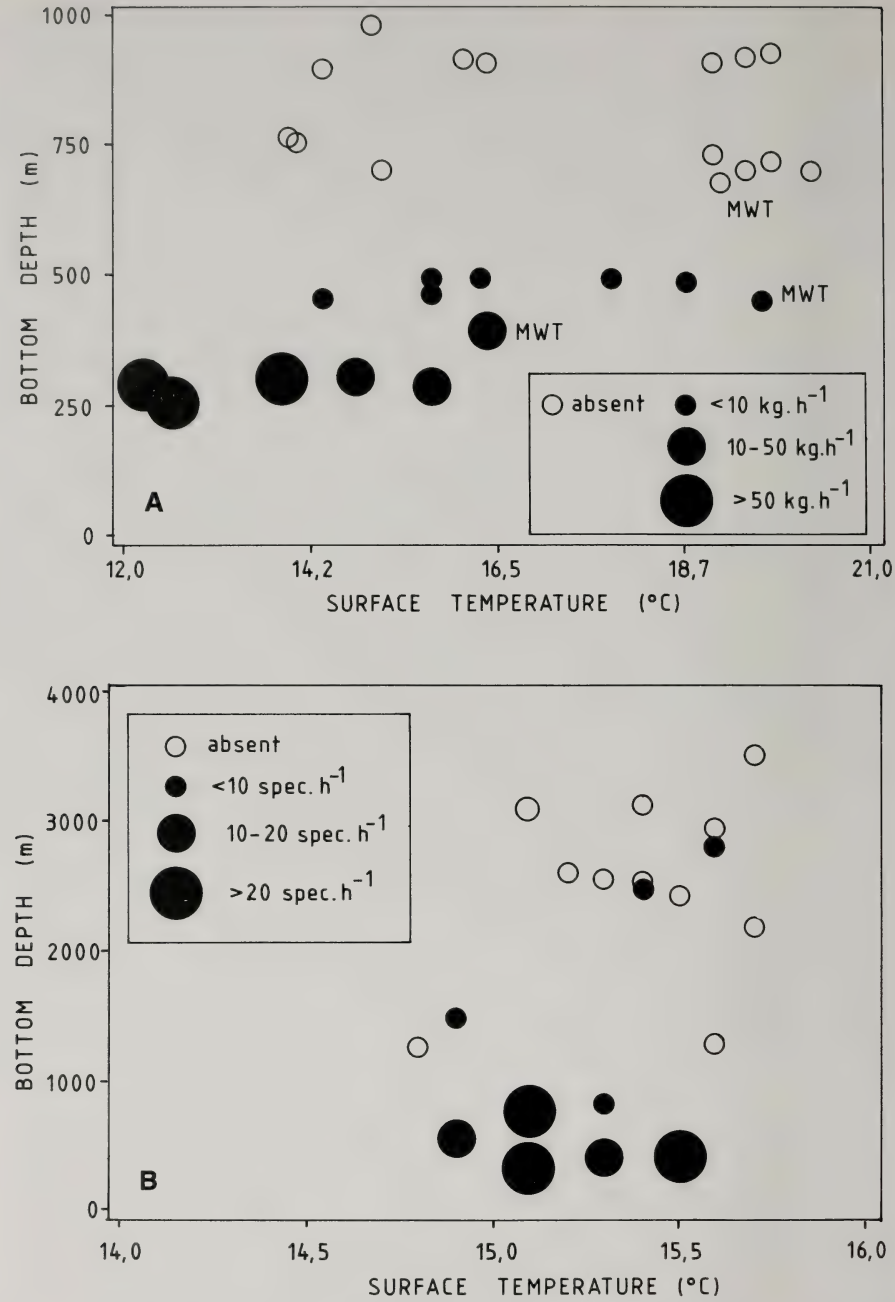


Fig. 8. Relative abundances of *Lampanyctodes hectoris* in relation to bottom depth and sea-surface temperature: (A) epibenthic + midwater Engels-308 stations from Cruise 060; (B) RMT-8 stations from Cruise 023. MWT = midwater Engels-308 haul.

prolonged upwelling (Hutchings *et al.* 1986) and would allow shelf-edge populations of oceanic pelagic fish species (particularly myctophids) to reap the benefit of the upwelling productivity, as has been suggested for the Mauritanian Upwelling region (Badcock 1981). In the latter region, the zooplankton biomass (principally copepods) is higher over the outer shelf and slope than the inner shelf (Blackburn 1979), whereas in the southern Benguela region copepod biomass is highest over the shelf (Pillar 1986) and is associated both with enhanced primary productivity and pelagic fish production on the shelf (Shannon & Field 1985). Although demersal fishes, which are indicative of less-productive areas (Mills & Fournier 1979), are said to dominate the slope regions (Shannon & Field 1985), high catch-rates for shelf-edge myctophid species (mainly *Diaphus hudsoni*, *Symbolophorus boops* and *Symbolophorus barnardi*) during Cruise 060 in the southern Benguela (Table 5) approximate similar values for equivalent shelf-edge species (mainly *Diaphus dumerilii* and *Diaphus taaningi*) in the Mauritanian Upwelling region (Gjøsaeter & Blindheim 1982, table 77).

During winter the frequency of active upwelling is reduced in the southern Benguela region (Lutjeharms & Meeuwis 1987). The front becomes weaker and relaxes, with a consequent decline in sea-surface temperature values. The seaward extent of cooler waters (less than 16 °C) increases up to 220 km off-shore in association with a seaward expansion of the upwelling filaments (Parrish *et al.* 1983; Shelton *et al.* 1985; Lutjeharms & Stockton 1987). This results in the formation of a wider productive zone than in summer but one in which near-surface chlorophyll concentrations are lower (Shannon *et al.* 1985). The standing stock of plankton may increase in winter but the production may be less because of low light levels and reduced nutrient regeneration (Shelton *et al.* 1985). Evidence from thermal infra-red satellite imagery during August 1984 (Fig. 3B) indicates that those stations, which were clustered as Group II in the above analysis (stations 4 (1), 5 (1), 7 (1), 8 (1), 9 (1)), are all situated seaward of the surface expression of the fronts. Absolute sea-surface temperatures for these stations ranged between 14,9 °C–15,5 °C and are similar to the 14,8 °C–15,7 °C range for those stations clustered as Group I. By contrast, montage of the station positions in relation to the location of the fronts during August 1983 (Fig. 3A) reveals that all stations were inshore of the front at this time. Absolute sea-surface temperatures for these stations were not available for this cruise. These findings therefore suggest that during winter the off-shore distribution of *Lampanyctodes hectoris* is unrelated to the position of the surface front.

In winter, feeding intensity may be reduced (Young & Blaber 1986) and the lipid composition of adult *Lampanyctodes hectoris* decreases in association with reproductive activity (Hulley & Prosch 1987). CELP Survey data indicated that spawning did not occur to any great extent in-shore of the 14 °C surface isotherm and that egg abundances were greatest along the shelf break between the 300-m and 1 000-m isobaths (Shelton 1986, fig. 5.28). Off South West Africa–Namibia, where the seasonality of upwelling is less marked than in the southern

Benguela region (Shannon 1985; Lutjeharms & Meeuwis 1987), spawning also takes place in winter–early spring (August–November) (Ahlstrom *et al.* 1976). The latter authors have reported that more than 60 per cent of the larvae occurred where sea-surface temperatures ranged between 14,0 °C and 15,5 °C, and larval abundances were greatest seaward of the 100 fm (183 m) isobath. Since both data sets imply the presence of large populations of spawning adults beyond the shelf break during the winter season, it seems not unlikely that there is a shift in the distribution of the species to deeper waters at this time. The analyses of our data given above would confirm this supposition. Plots of the relative abundances of *Lampanyctodes hectoris* at RMT–8 stations from Cruise 023 (winter) in relation to bottom depth and sea-surface temperature (Fig. 8B) indicate that, whereas the species occurred over bottom depths to about 3 000 m, they were most abundant at depths shallower than 760 m, where sea-surface temperatures ranged between 14,9 °C and 15,5 °C. The temperature range matches that proposed for the larval distribution patterns (Ahlstrom *et al.* 1976; Shelton 1986).

In summary, it is postulated that the summer distribution of *Lampanyctodes hectoris* mainly in-shore of the 300-m isobath is related to the availability of suitable quantities of food in the water column. During this time a lipid energy reserve is metabolized for use in later spawning activity. The distribution of these food items in the southern Benguela region is itself governed by the dynamics of the frontal system which develops during upwelling and which restricts plankton-rich waters to the east of the shelf break. Sinking at or breach-

TABLE 7

Minimum depth of water column for pelagic and benthic captures of oceanic Myctophidae during the Phyllosoma, Anchovy Acoustic and Hake surveys by SFRI. BDepth = bottom depth; FDepth = fishing depth, No. specs = number of specimens.

Zone	Month	Cruise	Gear	Station No.	FDepth (m)	BDepth (m)	No. specs	Species
Pelagic	May	009	RMT-8	28-07	100-0	510	147 4	<i>Symbolophorus boops</i> <i>Symbolophorus barnardi</i>
	August	002	RMT-2	002035	100-0	540	1	<i>Diaphus hudsoni</i>
	August	011	RMT-8	P007	250-0	290	1	<i>Diaphus diadematus</i>
							1	<i>Diaphus hudsoni</i>
							1	<i>Lampanyctus alatus</i>
	August	023	RMT-8	1 (1)	120-20	525	1	<i>Lampanyctus australis</i>
Benthic	January	028	180'BT	A2304	354	354	1	<i>Diaphus ostenfeldi</i>
	January	039	180'BT	A345	740	740	72	<i>Symbolophorus boops</i>
	January	050	180'BT	A5276	407	407	1	<i>Lampadena notialis</i>
	July	022	180'BT	A1550	378	378	2	<i>Symbolophorus boops</i>
	July	033	180'BT	A2780	496	496	1	<i>Diaphus hudsoni</i>
							1	<i>Symbolophorus boops</i>
	July	046	180'BT	A4309	298	298	2	<i>Symbolophorus barnardi</i>
	July	054	180'BT	A5893	358	358	3	<i>Symbolophorus boops</i>

ing of the front may occur and may account for the apparent 'leakage' of the species to depths of 500 m. In winter the off-shore distribution expands and *Lampanyctodes hectoris* may be taken regularly over depths of 800 m, and less frequently over depths between 800 m and about 3 000 m. Although relaxation of the front takes place during this season, it seems unlikely that the distribution of the species is geared to the wider productive zone, since the decrease in lipid content would suggest a lower feeding intensity than in summer, and distribution of the species does not appear to be correlated with the positions of the winter fronts and the extent of nutrient-rich waters in the surface layers. Rather, it appears that adult populations of *Lampanyctodes hectoris* move to deeper water to spawn and catabolize lipids for the production of eggs.

Data at hand indicate that similar seasonal differences in distributional patterning are not evident for oceanic myctophids and suggest that water-column depth and, therefore, the potential to undertake diurnal migration may be the major factor governing the shoreward distribution of such species. During the summer months, the shallowest water-column depth (284 m) for pelagic captures of oceanic species (Table 5) is matched by an equivalent water-column depth (290 m) during winter (Table 7), whereas their occurrence in benthic hauls varies between 350–500 m in summer and 300–500 m in winter (Tables 5, 7).

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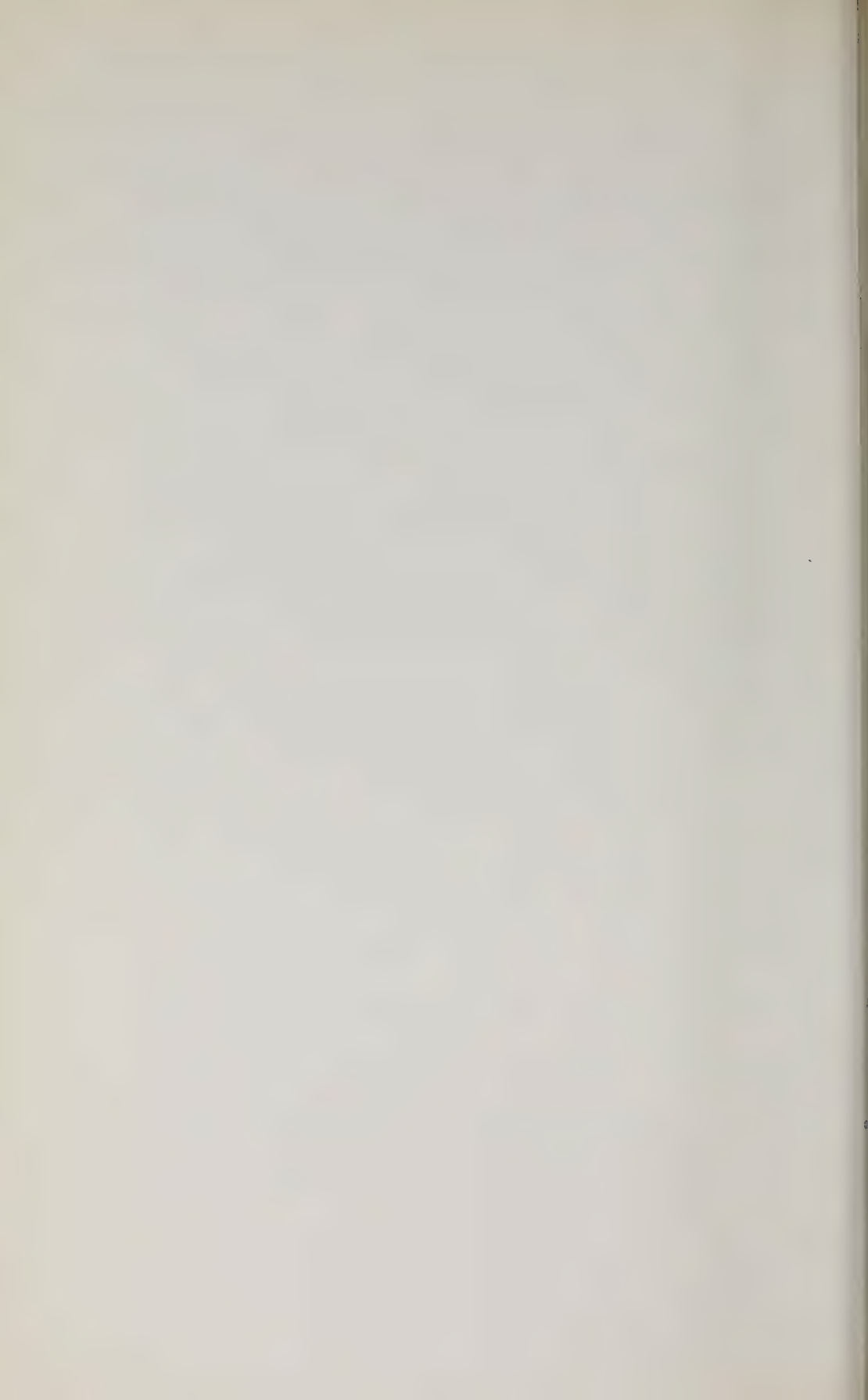
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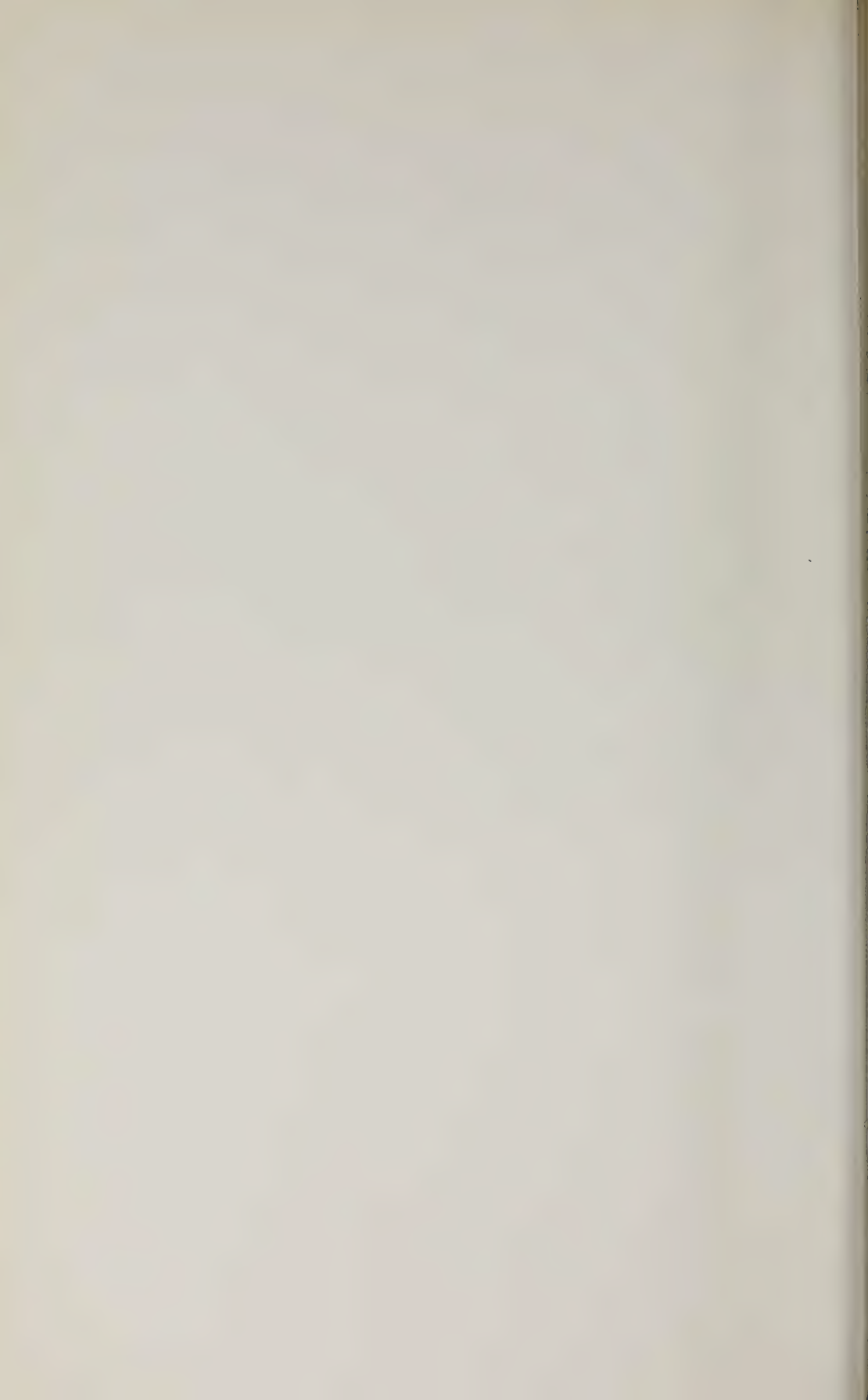
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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

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Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

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Note standard form of writing South African Museum registration numbers and date.

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- Scientific names, but not their vernacular derivatives
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Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

P. ALEXANDER HULLEY

&

J. R. E. LUTJEHARMS

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KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Annals and Magazine of Natural History* (13) 2 (17): 309–320.
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THIELE, J. 1910. Mollusca. B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika ausgeführt in den Jahren 1903–1905* 4 (15). *Denkschriften der medizinisch-naturwissenschaftlichen Gesellschaft zu Jena* 16: 269–270.

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FIRST RECORD OF AN EXTANT, SIGHTED,
SHALLOW-WATER SPECIES
OF THE GENUS *POSEIDONAMICUS* BENSON
(OSTRACODA) FROM THE CONTINENTAL
MARGIN OF SOUTH-WESTERN AFRICA

By
R. C. WHATLEY
&
R. V. DINGLE

Cape Town

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SPECIES OF THE GENUS *POSEIDONAMICUS* BENSON
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SOUTH-WESTERN AFRICA

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(With 11 figures and 3 tables)

[MS accepted 23 August 1988]

ABSTRACT

A new, sighted species of the ostracod genus *Poseidonamicus* (*P. panopsus* sp. nov.) is recorded living on the continental shelf and upper slope off south-western Africa in water depths between 120 m and 545 m. All previous records of the genus have been from water depths greater than 1 km. The discovery indicates that sighted species survived, in shallow-water, from the late Cretaceous/early Tertiary stocks when the genus originated in the SW Pacific area. The habitat of the new species is defined in terms of temperature, salinity, and dissolved oxygen values within the Antarctic Intermediate Water mass, where it forms part of the Benguela system, and associated cells of intense upwelling.

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INTRODUCTION

Cenozoic bathyal and abyssal deep-water ostracod faunas are characterized by distinctive cosmopolitan assemblages that include a number of ornate cytheracean taxa. Prominent amongst this group is the genus *Poseidonamicus*, which was originally erected by Benson (1972) to accommodate five species with a geological range ?Oligocene, Miocene–Recent, and which is extant

world-wide (Table 1). All the original species considered by Benson (1972), as well as two further Miocene species from the South Atlantic (Benson in Benson & Peypouquet 1983), were blind. Subsequent studies by Whatley and his colleagues (e.g. Whatley 1983, 1985; Whatley *et al.* 1983; Whatley *et al.* 1986) have extended the geological and geographical range of the genus (now known from Eocene to Recent). Despite the fact that Whatley *et al.* (1986) described one species with distinct but non-functional ocular structures (*P. ocularis* Whatley *et al.* 1986), all records of the genus to date have been from water depths known or estimated to be in excess of 1 km. *Poseidonamicus* has, therefore, up to now been considered typically a deep-water taxon, although the discovery of *P. ocularis* in Quaternary deep-water sediments prompted Whatley *et al.* (1986) to predict that a shallow-water ancestor existed at least until late Tertiary times in the SW Pacific region.

Table 1 lists the known species of the genus *Poseidonamicus*, as well as their geological and geographical ranges.

The most widely recorded species to date has been the type species *P. major* Benson, which has a known geological range Miocene to Recent (southern hemisphere), and a possible record in Oligocene of the NE Atlantic (Table 1). This species occurs in Pleistocene–Recent sediments off south-western Africa, where it has a known depth range 2 070–2 916 m (Dingle *et al.* in press).

Although the genus has been recorded from Tertiary sediments in the South Atlantic (*P. riograndensis* and *P. miocenica* from the Miocene of Deep Sea Drilling Project (DSDP) site 92—Benson & Peypouquet 1983), the main centre of evolutionary activity and the area where the genus has the longest geological record (Eocene to Recent) is the SW Pacific (e.g. Whatley 1985). No positive identifications of the genus have so far been made in the Tertiary strata of southern Africa (Frewin's 1987 record is considered questionable), so that the discovery of an extant population of a shallow-water species off southern Africa poses some interesting evolutionary, zoogeographical, and environmental questions.

A total of 119 valves of the new species (*P. panopsus*) have been recovered in 27 sediment samples from the continental shelf and slope off south-western Africa (Fig. 1, Table 2). All the samples were collected with a Van Veen grab by the Marine Geoscience Unit of the University of Cape Town from the research vessel *Thomas B. Davie*. (Sample numbers have a TBD prefix.)

TAXONOMY

All illustrated material is housed in the South African Museum under catalogue numbers prefixed SAM-PQ-MF. Abbreviations: ACA = anterior cardinal angle, AM = anterior margin, ATE = anterior terminal element, DM = dorsal margin, LV = left valve, MS = muscle scars, PM = posterior margin, PTE = posterior terminal element, RV = right valve, SCT = subcentral tubercle, VM = ventral margin.

TABLE 1
Spatial and temporal distribution of previously described species of *Poseidonamicus*.

Species	Age	Locality	Depth	Reference
<i>Poseidonamicus major</i> Benson, 1972	?Oligocene Miocene--Recent Miocene--?Recent Recent Quaternary Quaternary	NE Atlantic SW Pacific SW Atlantic SW Indian SE Atlantic E Pacific	bathyal--abyssal abyssal abyssal	Benson (1972) Benson (1972) Benson (1972) Benson (1972) Dingle, Lord & Boomer (in press) Benson (1972)
<i>Poseidonamicus minor</i> Benson, 1972	Recent	Indian, SE Pacific		Benson (1972)
<i>Poseidonamicus nudus</i> Benson, 1972	Recent	S Atlantic		Benson (1972)
<i>Poseidonamicus pintoi</i> Benson, 1972	Recent	Southern Ocean		Brady (1880), Benson (1972)
<i>Poseidonamicus viminea</i> (Brady, 1880)	Lower Miocene	DSDP site 92, S Atlantic		Benson & Peypouquet (1983)
<i>Poseidonamicus riograndensis</i> Benson, 1983	Middle Miocene	DSDP site 92, S Atlantic		Benson & Peypouquet (1983)
<i>Poseidonamicus miocenica</i> Benson, 1983	Miocene--Quaternary	SW Pacific		Whatley <i>et al.</i> (1986)
<i>Poseidonamicus anteropunctatus</i> Whatley <i>et al.</i> , 1986	Quaternary	SW Pacific		Whatley <i>et al.</i> (1986)
<i>Poseidonamicus ocularis</i> Whatley <i>et al.</i> , 1986	Pliocene--Quaternary	SW Pacific		Whatley <i>et al.</i> (1986)
<i>Poseidonamicus praeunus</i> Whatley <i>et al.</i> , 1986	late Cenozoic	N Atlantic		Whatley & Coles (1987)
<i>Poseidonamicus punctatus</i> Whatley <i>et al.</i> , 1986	Quaternary	SW Pacific		Whatley <i>et al.</i> (1986)
<i>Poseidonamicus robustus</i> Whatley <i>et al.</i> , 1986	Eocene--Oligocene	SW Pacific		Whatley <i>et al.</i> (1986)
<i>Poseidonamicus nudis</i> Whatley <i>et al.</i> , 1986	Eocene--Quaternary	SW Pacific		Whatley <i>et al.</i> (1986)
<i>Poseidonamicus</i> sp. Whatley <i>et al.</i> , 1986	Pliocene	Ita Mai Tai guyot, SW Pacific		Whatley <i>et al.</i> (1986)
<i>Poseidonamicus</i> cf. <i>P. major</i> Benson, 1972	late Cenozoic	N Atlantic		Whatley & Coles (1987)
<i>Poseidonamicus</i> cf. <i>P. pintoi</i> Benson, 1972	late Cenozoic	N Atlantic		Whatley & Coles (1987)
<i>Poseidonamicus</i> sp. Whatley & Coles, 1987	late Cenozoic	N Atlantic		Whatley & Coles (1987)
<i>Poseidonamicus</i> sp. nov. Coles & Whatley, 1989	Oligocene	NE Atlantic		Coles & Whatley (1989)

TABLE 2

Sample sites.

TBD	Latitude °S	Longitude °E	Depth (m)	No. ostracod valves	No. <i>P. panopsus</i>	Percentage <i>P. panopsus</i>	Percentage mud
Walvis Shelf							
3769	22,250	13,233	223	39	1	3	9,3
Orange Shelf							
2752	29,783	16,017	170	374	1	0,1	90,4
2973	28,417	15,000	173	1 460	1	0,1	82,4
2975	28,417	14,583	180	892	1	0,1	76,4
2925	28,900	15,367	183	284	3	1	25,8
2974	28,417	14,800	186	2 011	2	0,1	79,7
2840	30,917	15,700	205	108	9	8	8,7
2736	29,950	15,417	205	555	6	1	83
2717	30,400	16,433	218	112	4	4	33
2703	30,133	15,433	220	239	7	3	76,4
2485	30,917	16,000	227	114	2	2	19,6
2719	30,450	16,067	240	140	13	10	30,2
2361	31,313	16,858	241	70	9	13	64
2884	29,317	14,717	252	159	2	1	22
2691	30,533	15,617	265	43	1	2	27,4
2690	30,517	15,833	271	137	12	9	23
2460	31,233	16,625	272	39	1	3	90
2459	31,233	16,383	300	299	5	2	85,7
2976	28,417	14,383	350	18	2	11	92,5
2447	31,925	16,467	350	49	1	2	22,9
3577	31,367	16,083	453	96	1	1	84,2
SW Cape							
6823	34,093	18,215	120	1 098	11	1	—
3587	33,995	18,148	140	167	7	4	25,7
6825	34,090	18,173	160	222	10	5	—
1691	34,567	18,483	220	516	5	1	55
1694	34,750	18,327	425	31	1	3	72,4
1697	34,767	18,250	545	112	1	1	62

Phylum CRUSTACEA Pennant, 1777

Class OSTRACODA Latrille, 1806

Order PODOCOPIDA Müller, 1894

Suborder PODOCOPINA Sars, 1866

Superfamily CYTHERACEA Baird, 1850

Family *Trachyleberididae* Sylvester-Bradley, 1948Subfamily *Thaerocytherinae* Hazel, 1967Genus *Poseidonamicus* Benson, 1972

The genus was erected by Benson (1972) to accommodate a number of deep-sea, reticulate to virtually smooth, holamphidont-hinged species. They are characterized by certain features of their carapace morphology, such as the absence of an ocular rib, the presence of regular, vertically aligned fossae and muri posteromedianly, and a reticulate to punctate area medianly, the two areas being separated by a subvertical loop in the region of the adductor scars. These

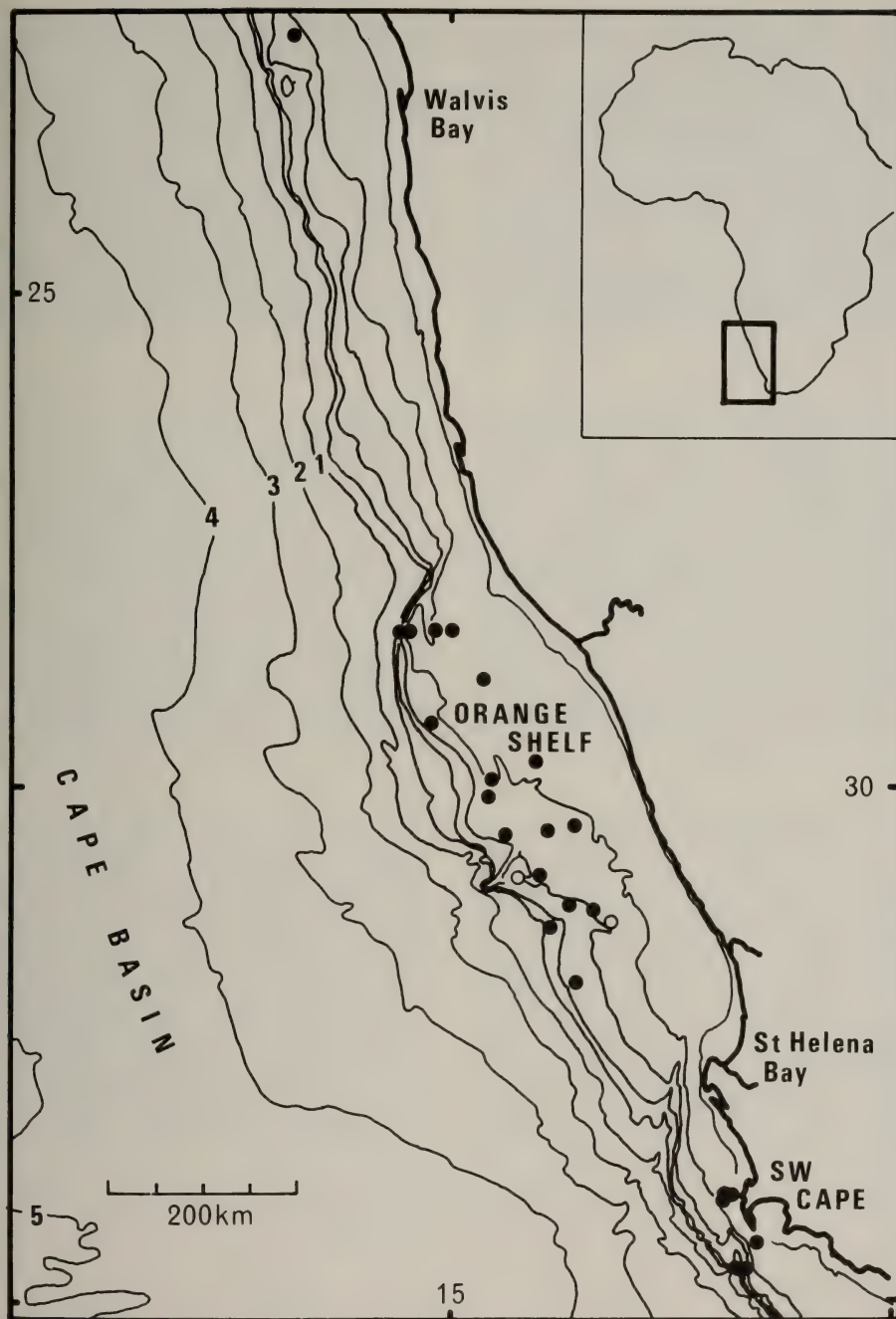


Fig. 1. Locations of sediment samples containing *Poseidonamicus panopsus* sp. nov. on the continental margin off south-western Africa. Isobaths at 100 m to 500 m and 1 km to 5 km. Sample numbers and locations are listed in Table 2. Open circles are sites with living specimens. Inset shows location of study area.

features are present even in smooth species, such as *P. nudus*, if viewed in transmitted light. Benson (1972) based the genus on five species (see Table 1; type species *P. major* Benson, 1972), and the diagnosis has been amended by Whatley *et al.* (1986) on the basis of their study of six additional species from the SW Pacific (Table 1).

Poseidonamicus panopsus sp. nov.

Figs 2-3, 4A-E, 5C

Bradleya? sp. Boomer, 1985: 42-43, pl. 3 (figs 35-36).

Derivation of name

Greek *panops*, all seeing. With reference to the well-developed ocular structures of this obviously sighted species, and also because Gods and their friends tend to be all seeing.

Material

Holotype SAM-PQ-MF0502, female LV, TBD 2719, 240 m.

Paratypes SAM-PQ-MF0503, female LV, TBD 2719, 240 m.

SAM-PQ-MF0504, ?male RV, TBD 2690, 271 m.

SAM-PQ-MF0505, ?male LV, TBD 2459, 300 m.

SAM-PQ-MF0506, female carapace, TBD 2840, 205 m.

SAM-PQ-MF0507, juvenile LV, TBD 2840, 205 m.

SAM-PQ-MF0508, juvenile RV, TBD 6823, 120 m.

Dimensions (mm)

	<i>length</i>	<i>height</i>	<i>width</i>
MF0502	0,91	0,51	—
MF0503	0,89	0,52	—
MF0504	0,92	0,49	—
MF0505	0,89	0,48	—
MF0506	0,85	0,47	0,48
MF0507	0,64	0,37	—
MF0508	0,70	0,39	—

Diagnosis

A medium-sized, sighted species of *Poseidonamicus* with large hemispherical eye tubercle and distinct internal ocular sinus. Ornament reticulate with large open fossae, the solae of which are secondarily reticulate. SCT prominent; medianly inflated. Dorsal margin with prominent anterior and posterior hinge ears in LV.

Description

External features. Medium-sized (see relative size scale for genus, Whatley *et al.* 1986: 388), thick-shelled and robust. Subrectangular in lateral view; strongly inflated medianly and bluntly acuminate terminally in dorsal view. AM

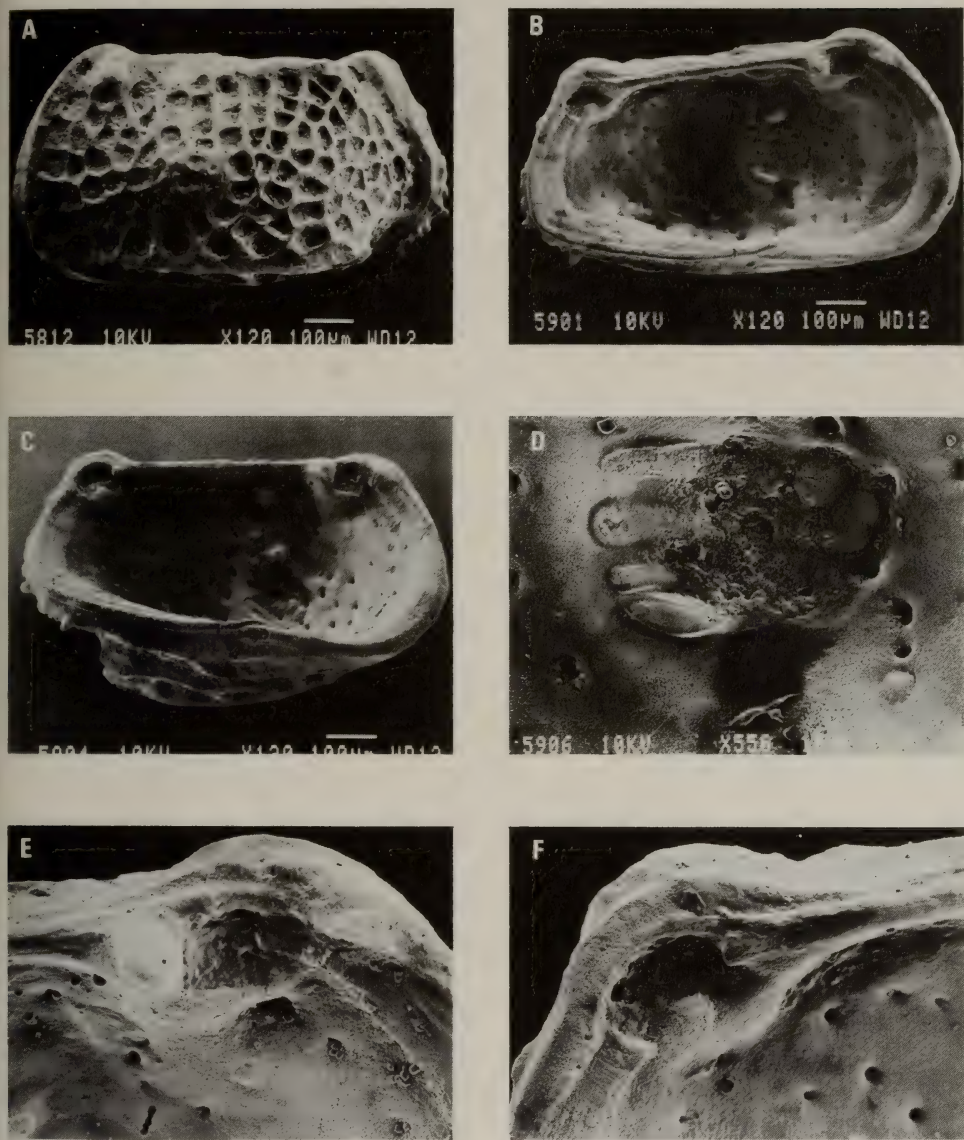


Fig. 2. *Poseidonamicus panopsus* sp. nov. SAM-PQ-MF0502, holotype, LV, female, TBD 2719, 240 m. A. External view. B. Internal view. C. Oblique internal view. D. Central muscle scars. E. ATE. F. PTE.

Scale bars: A-C = 100 microns; D-F = 10 microns.

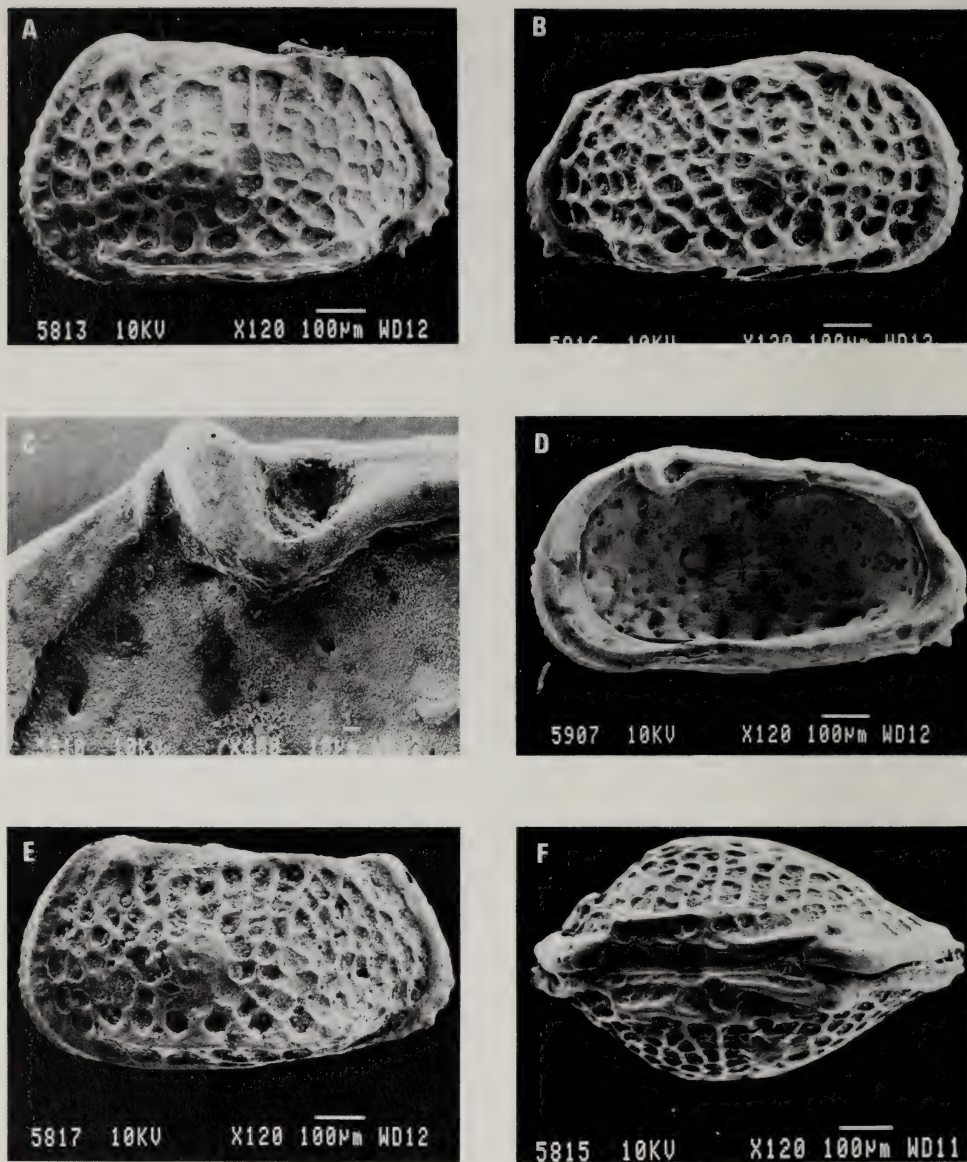


Fig. 3. *Poseidonamicus panopsus* sp. nov. A. SAM-PQ-MF0503, LV, female, TBD 2719, 240 m. B-D. SAM-PQ-MF0504, RV, male, TBD 2690, 271 m. B. External view. C. ATE.

D. Internal view. E. SAM-PQ-MF0505, LV, male, TBD 2459, 300 m.

F. SAM-PQ-MF0506, carapace, dorsal view, TBD 2840, 205 m.

Scale bars: A-B, D-F = 100 microns; C = 10 microns.

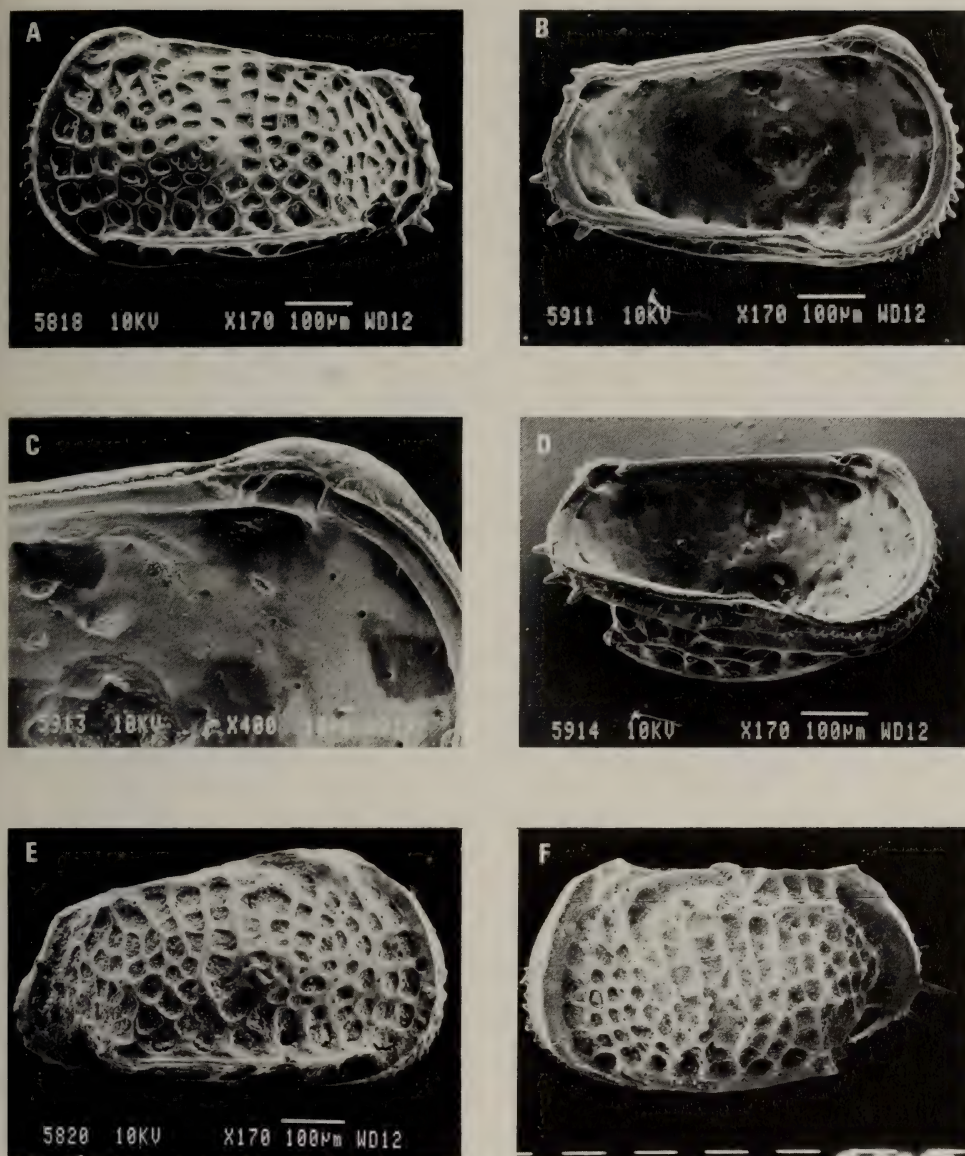


Fig. 4. A-E. *Poseidonamicus panopsus* sp. nov. A-D. SAM-PQ-MF0507, LV, juvenile, TBD 2480, 205 m. A. External view. B. Internal view. C. ATE. D. Oblique internal view. E. SAM-PQ-MF0508, RV, juvenile, TBD 6823, 120 m. F. *Poseidonamicus major* Benson, 1972, SAM-PQ-MF0495, LV, TBD 6851, 2 916 m, continental slope off south-western Africa. Scale bars: A-B, D-F = 100 microns; C = 10 microns.



Fig. 5. Comparison of central MS patterns. A. *Poseidonamicus major* Benson, 1972, SAM-PQ-MF0497, RV, TBD 6851, 2 916 m, continental slope off south-western Africa (Dingle *et al.* in press). B. *Poseidonamicus major* Benson, 1972, USNM 174354, RV, IIOE 363B, 2 995 m, Mozambique Channel (Benson 1972). C. *Poseidonamicus panopsus* sp. nov. SAM-PQ-MF0504, RV, TBD 2690, 271 m.

Scale bars = 100 microns.

asymmetrically rounded in RV; with more pronounced antero-dorsal slope in LV; bearing numerous small marginal denticles. PM with blunt apex below mid-height and with short, convex denticulate postero-ventral slope and longer straight or concave postero-dorsal slope. DM straight with prominent anterior and posterior hinge ears in LV, particularly in the female. VM straight to very gently convex. Greatest height at the ACA, greatest length just below mid-height; greatest width just behind mid-length. Eye tubercle large, hemispherical and prominent, more peripheral in the RV than the LV due to the presence of the hinge ear in the latter. Ornament reticulate with large open fossae of fairly regular size, which are more circular anteriorly than elsewhere. Muri somewhat preferentially aligned vertically postero-dorsally, and horizontal to subradiate anteriorly. Solae secondarily reticulate in a radiate pattern. SCT slightly elevated in the region of the adductor scars, bearing small deep fossae and being embraced posteriorly and ventrally by the mural loop characteristic of the genus. Marginal rims prominent anteriorly and posteriorly; smooth except for a thin ridge along their crests. Vento-lateral ridge prominent and sub-ponticulate. A dorsal ridge, divided into two parts, extends subparallel to the dorsal margin.

Internal features. Calcareous inner lamella rather narrow, but strongly developed, selvage prominent. Avestibulate. Internal ocular sinus distinct, open in juveniles, somewhat restricted at its base in adults. Hinge holamphidont. MS comprising four undivided adductors, two frontals and two mandibular scars.

Remarks

This species differs from all other known species of the genus by possessing a prominent eye tubercle, a distinct internal ocular sinus, an inflated carapace, and in details of its ornamentation. The only other species of *Poseidonamicus* with ocular features is *P. ocularis* Whatley *et al.*, 1986. The latter species, from the Quaternary of three DSDP sites in the southern part of the area between Australia and New Zealand, was so named because it has a small (much smaller than that of *P. panopsus* sp. nov.) but prominent eye tubercle and an internal ocular sinus. The two species, despite the fact that they both possess strong hinge ears in the LV, can readily be distinguished in that they possess quite different ornament, and because *P. ocularis* lacks a SCT.

Although the external morphology of the new species differs significantly from *P. major* Benson and there is no possibility of confusion, we include a comparison of the central MS of the two species, because *P. major* is the only other representative of the genus recorded from southern Africa (Mozambique Channel, Benson 1972; Cape Basin, Dingle *et al.* in press). The MS of the two species are very similar (Fig. 5), with the anterior scars consisting of an ovate dorsal scar and a partially subdivided ventral scar, whereas the adductors are all elongate/ovate, with a 'dog's bone'-shaped second scar. The third scar of the adductor quartet in *P. major* is relatively longer than in *P. panopsus*.

Range

Pleistocene–Recent.

DISCUSSION

The discovery of a sighted species of *Poseidonamicus* living on the continental shelf off south-western Africa has a number of important implications for understanding the evolution of the genus.

DISTRIBUTION AND ECOLOGY

Poseidonamicus panopsus sp. nov. has been found on the continental margin of south-western Africa between latitudes 22°S and 35°S, where it has a depth range of 120 m (mid-continental shelf) to 545 m (upper continental slope) (Fig. 1, Table 2). With the exception of sample TBD 3769 (NW of Walvis Bay), however, all the occurrences lie south of 28°S, and cluster into two distinct groups: on the Orange Shelf (28°S–32°S); and off the SW Cape (34°S–35°S). The isolated site off Walvis Bay consists of one valve, and this is separated by 6 degrees of latitude (650 km) from the Orange Shelf population.

TABLE 3

Distribution of *Poseidonamicus panopsus* sp. nov. (values are means for n sites).

Area (n)		Percentage <i>P. panopsus</i>	Percentage mud	Depth (m)	Range
A.	Walvis Shelf (1)	3	9	223	223
B.	Orange Shelf (20)	4	56	248	170-453
C.	SW Cape (6)	3	54*	268	120-545
D.	Overall (27)	3	53*	251	120-545

Living specimens occur at two sites on the Orange Shelf. At these sites the following parameters apply:

	Percentage <i>P. panopsus</i>	Percentage mud	Depth (m)
	8	9	205
	13	64	241

* = excludes samples 6823 and 6825 for which no mud values are available.

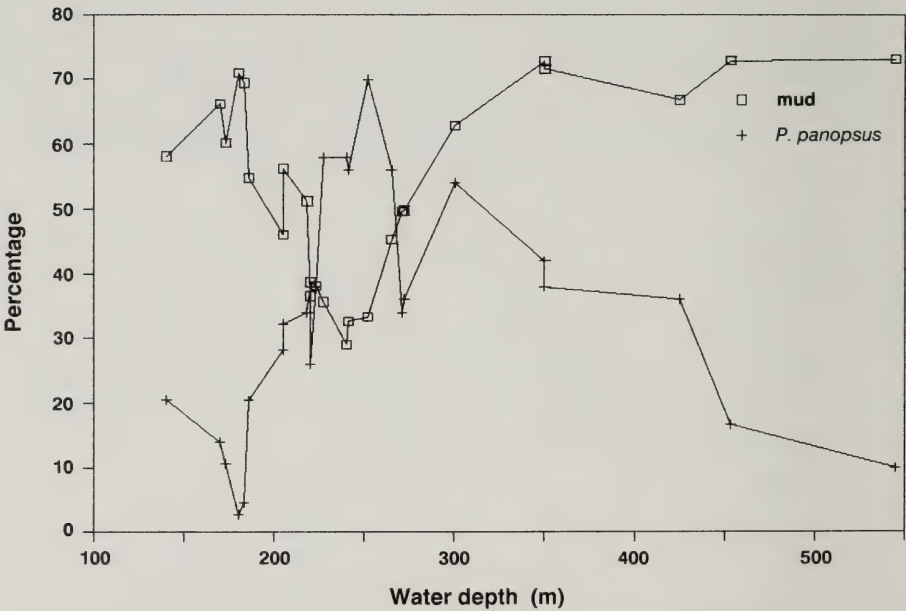


Fig. 6. Mud content of sediment samples and relative abundance of *Poseidonamicus panopsus* sp. nov. (percentage of ostracod fauna $\times 10$) plotted against water depth. Mud and percentage ostracod values are smoothed 5-point means. Samples TBD 6823 and TBD 6825 have not been included (no analysis of mud contents are available). Note the inverse relationship between the mud content and percentage *P. panopsus*, with peak values of the latter on the outer continental shelf (c. 250 m water depth).

Table 3 lists some of the parameters of the areas of occurrence. In the Orange Shelf and SW Cape populations, the species has a similar depth range (170–453 m, and 120–545 m, respectively), and the mean mud contents of the sediments in which the species is recorded (53 % and 54 %) and the mean abundance of the species (4 % and 3 %) are also very close. These two areas are separated by approximately 200 km of shelf which is barren of *P. panopsus*. Plots of the abundances of the species (as percentage of the ostracod population) against the mud contents of the sea-floor sediments (Fig. 6) indicate that the species peaks (up to 60 % total ostracod population) at about 250 m water depth, where the mud content of the sediment is lowest (mean of 30 %). On the adjacent inner shelf and outer shelf/upper slope, where the mean mud contents are >60 %, the abundance of *P. panopsus* rapidly declines. This indicates that the species is generally not tolerant of high mean mud values (>70 %). However, the fact that the region between the Orange Shelf and SW Cape populations, which is barren of the species, has a mean mud content of 30 per cent (compared to 50 % for all sediments in the two populated areas) suggests that a minimum mean mud threshold (30 %) is one of the factors necessary to sustain the species.

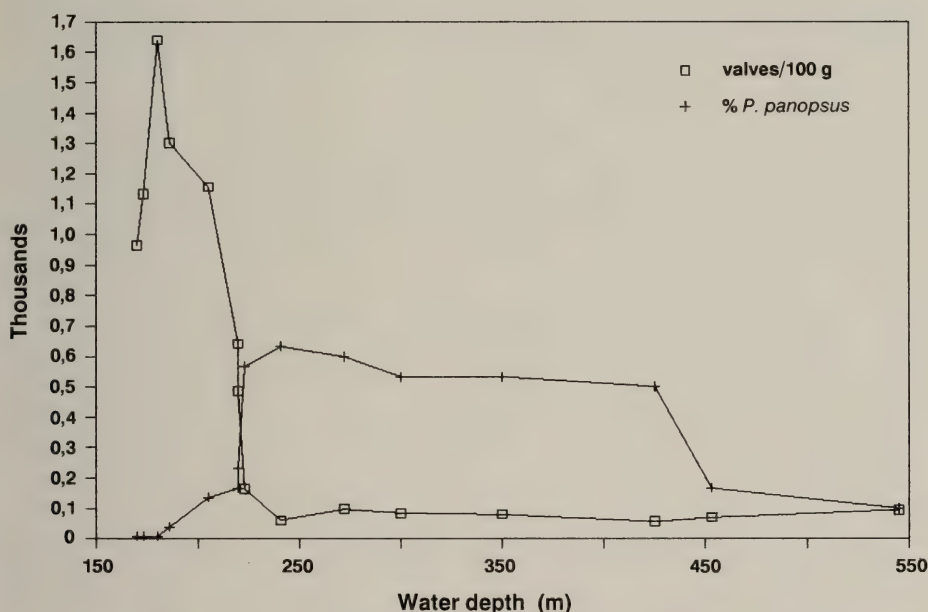


Fig. 7. Abundance of ostracod population (number of valves/100 g sediment) and relative abundance of *Poseidonamicus panopsus* sp. nov. (percentage of ostracod fauna $\times 100$) plotted against water depth. Ostracod population and *P. panopsus* values are smoothed 3-point means. Samples TBD 6823 and TBD 6825 are not included (no ostracod population abundance values available). Note the high ostracod population values on the mid-shelf, which decline rapidly into deeper water, with a concomitant increase in relative abundance of *P. panopsus*.

A further limiting factor within the two main *P. panopsus* population centres is the abundance of the whole ostracod fauna (Fig. 7). Mean values (measured as number of valves/100 g of original dry sediment) peak on the inner shelf (>500 valves/100 g in <200 m water depths), and fall rapidly towards the outer shelf and slope. Concomitant with this decline in the overall abundance of the ostracod fauna, there is a marked increase in the percentage of this fauna made up by *P. panopsus*. This trend suggests that the species has limited toleration of competition from large numbers of individuals belonging to other species, although at present the nature of this factor remains unknown.

Living specimens were collected at two locations (TBD 2840 and 2361), both in the Orange Shelf area, but plots of the population structure show that in both this area, and within the SW Cape occurrences, the mean percentages of adult valves varies between 20 and 70 per cent, with the higher values concentrated in water depths between 200 m and 250 m in the Orange Shelf area (Figs 8, 9). These assemblages of mixed adults and juveniles suggest that both the main areas of occurrence reflect viable extant populations. The isolated site off Walvis Bay is a single dead adult valve, and we are not in a position to determine its true status. Its transportation as a relatively fragile clast 650 km from the the Orange Shelf population seems unlikely, but we have good sample coverage over the whole of the adjacent continental shelf, and it is equally unlikely that a population centre larger than 300 km² would have been undetected.

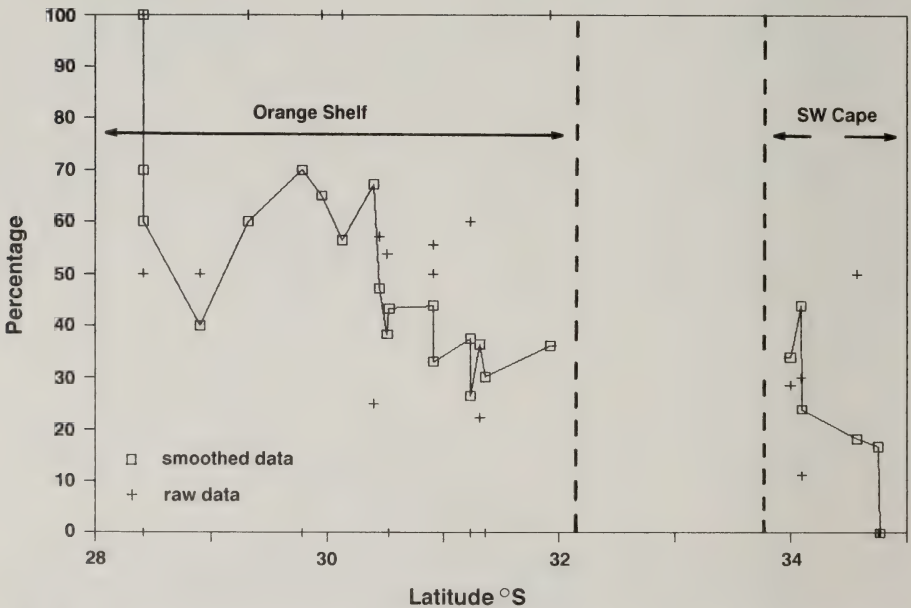


Fig. 8. Percentage of adult valves of *Poseidonamicus panopsus* (raw and smoothed 5-point means) plotted against latitude. Sample TBD 3769 off Walvis Bay is omitted. Mean values: Orange Shelf = 49 per cent adult, SW Cape = 29 per cent adult.

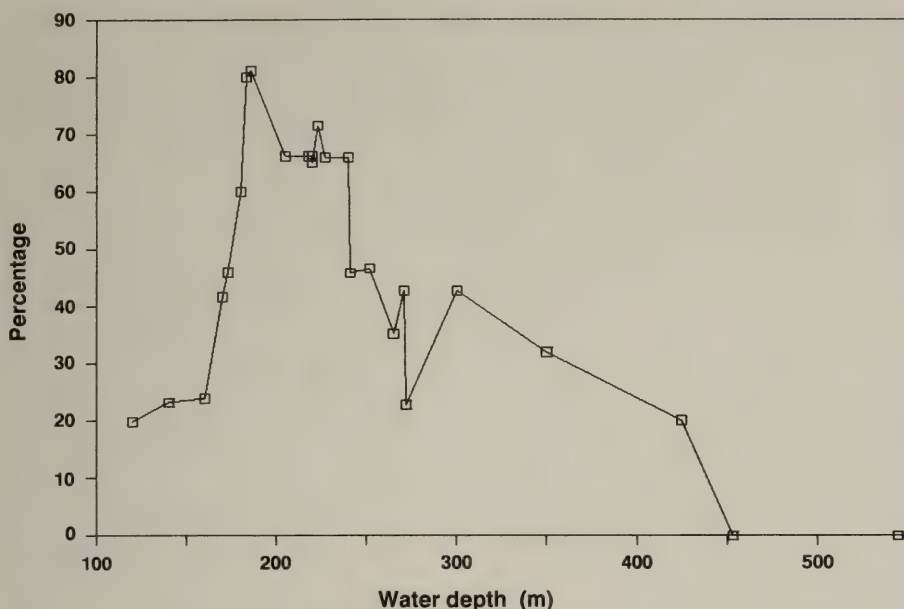


Fig. 9. Percentage of adult valves of *Poseidonamicus panopsus* (smoothed 5-point means) plotted against water depth. Note that peak values ($>60\%$) lie around 200 m water depth, which is slightly shallower than the peak values of abundance of the species (Fig. 6—250 m).

The three deepest sites at which the species was recovered (TBD 1694, 425 m; TBD 3577, 453 m; and TBD 1697, 545 m) all consist of single juvenile valves, which possibly indicate allochthonous occurrences due to downslope postmortem transportation. If this is the case then the true lower depth limit of the species is 350 m.

The oceanographic climate off south-western Africa is complex, with large-scale upwelling over the continental shelf area (Shannon 1985). Figure 10 shows sea-floor variations in temperature, salinity, and dissolved oxygen across the continental margin at the southern end of the Orange Shelf (32°S). The upper depth limit of *P. panopsus* on the Orange Shelf is 170 m, and this occurs at approximately the same depth as two important changes in physico-chemical parameters: the base of the inner shelf thermocline (c. 13°C—<9.5°C), and the western limit of the continental shelf low dissolved oxygen zone. The slightly shallower upper depth limit (120 m) off the SW Cape (34°S) may reflect somewhat lower sea-floor temperatures at shallower depths: the 9°C isobath intrudes to depths of 100 m for much of the year in this area (see Shannon 1985, fig. 21).

Low dissolved oxygen values (<2 ml/l) may also be important limiting factors in the latitudinal distribution of the species. A major source of oxygen deficient water lies to the north of the Orange Shelf, where Chapman & Shannon (1985)

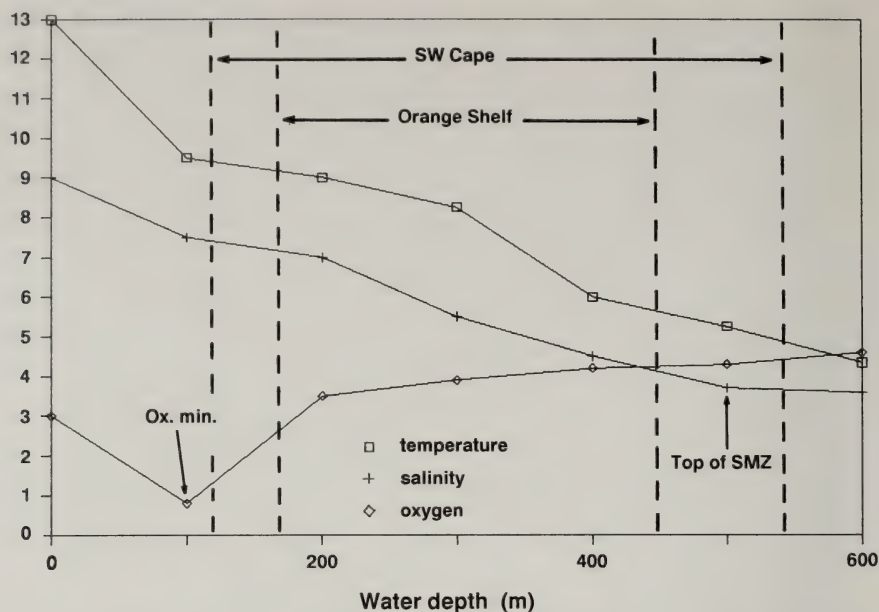


Fig. 10. Variations in water temperature, salinity, and dissolved oxygen on the sea floor along a transect across the continental margin at approximately 32°S. Data from Fuglister (1960), Stander (1964), Shannon (1966, 1985), Shannon & Van Rijswijk (1969). Depth ranges of *P. panopsus* on the Orange Shelf and off the SW Cape are indicated by arrows. Note that the western limit of the 'oxygen deficient zone' (<2 ml/l, as defined by Chapman & Shannon 1985) lies at approximately 180 m water depth (Stander 1964). This is somewhat deeper than predicted by the straight line connecting the two data points used to create the dissolved oxygen curve.

Parameters: temperature = °C, salinity = $[(\text{‰} - 34) \times 10]$, dissolved oxygen = ml/l. Abbreviations: oxygen = dissolved oxygen, Ox. min. = oxygen minimum, SMZ = salinity minimum zone of AAIW.

identified a double low on the continental shelf, whereas a smaller, but persistent source is centred on St Helena Bay. We suspect that the latter may contribute to the *P. panopsus*-barren region between 32°S and 34°S. Similarly, the oxygen-low area immediately off the Orange River mouth (Chapman & Shannon 1985, fig. 6) may be a factor restricting the species to water deeper than 170 m on the Orange shelf (compared to 120 m off the south-western Cape).

At the lower depth limit (545 m or 350 m, depending on whether our three deepest specimens are allochthonous), gradients in the variation of sea-floor temperature and dissolved oxygen are relatively low, but Shannon (1985) has located the top of the salinity minimum zone (SMZ) within the Antarctic Intermediate Water mass (AAIW) at approximately 600 m along most of the continental margin of south-western Africa. Data in Fuglister (1960) show this phenomenon to be closer to 500 m at 32°S (Fig. 10), and Dingle *et al.* (in press) have recognized the bottom of the SMZ (at about 950 m) to be a major faunal barrier, separating neritic and bathyal ostracod faunas. We suspect that the lower

depth limit of *P. panopsus* is regulated by the level of the top of the SMZ within the AAIW mass.

In summary, we believe that the following environmental parameters influence the distribution of *Poseidonamicus panopsus* sp. nov.:

1. The species prefers a mud content in the sediment of between 30 and 50 per cent, with the lower value limiting its distribution.
2. It is most abundant where it lives within ostracod populations with low abundances (<400 valves/100 g).
3. Limiting water temperatures are approximately 9,0°C–5,8°C.
4. Limiting salinities are 34,70–34,40‰.
5. Limiting dissolved oxygen values are 2,7–4,2 ml/l.
6. The species tolerates the nutrient-rich conditions of the upwelling cells associated with the Benguela system, but where these cells result in intense biological productivity and oxygen deficiencies in the water column (to the north of the Orange Shelf area, and between the Orange Shelf and the SW Cape area), dissolved oxygen values on the sea floor are too low for its survival.

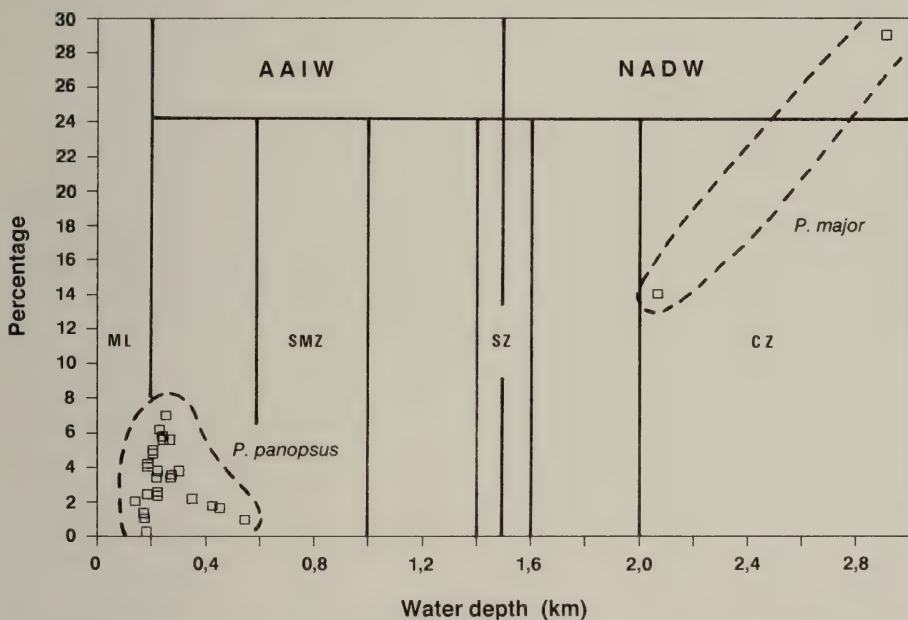


Fig. 11. Relative abundances of *Poseidonamicus panopsus* sp. nov. and *Poseidonamicus major* Benson (percentage of ostracod population) plotted against water depth. The populations of the two species are separated by 1 500 m of water on the continental slope which contains the following physico-chemical barriers: salinity minimum zone of the Antarctic Intermediate Water mass; the shear zone of the Antarctic Intermediate Water/North Atlantic Deep Water masses boundary; and the top of the core of the North Atlantic Deep Water. Note also that *Poseidonamicus major* is a more important component of the abyssal ostracod fauna than is *P. panopsus* of the neritic ostracod fauna (means 22 % and 3,3 %, respectively).

Abbreviations: AAIW = Antarctic Intermediate Water; CZ = core zone; ML = mixed layer; NADW = North Atlantic Deep Water; SMZ = salinity minimum zone; SZ = shear zone.

Dingle *et al.* (in press) discuss some of the factors that may be responsible for confining various deep-water (>950 m) ostracod assemblages to their respective depth ranges. They concluded that the upper depth limit of *P. major* off south-western Africa is probably controlled by the position of the top of the core zone of the North Atlantic Deep Water mass (NADW), above which higher temperatures (>3,0°C) and lower salinities (<34,86‰) occur. Figure 11 shows the depths and abundances (as percentage of ostracod fauna) of samples containing *Poseidonamicus major* and *P. panopsus* off south-western Africa and emphasizes that, although the two species are both extant, they are separated by 1 500 m of water column that contains two major barriers to faunal mixing: the SMZ of the AAIW; and the contact zone between the AAIW and the NADW. As Dingle *et al.* (in press) point out, both these are powerful barriers that control the Neritic/Upper Bathyal, and Upper Bathyal/Lower Bathyal faunal boundaries, respectively. In addition, the top of the NADW core regulates the Lower Bathyal/Abyssal faunal boundary. Because the water masses that give rise to the controlling physico-chemical gradients have been in existence since at least mid-Tertiary time, the separation of the two *Poseidonamicus* species off south-western Africa is likely to have been a long-term phenomenon.

GENERAL CONSIDERATIONS

Benson (1972: 21), apart from speculating that the ancestry of *Poseidonamicus* 'reaches far back into the Cretaceous', could not, at the time, suggest a possible ancestor for the genus. Subsequently, Whatley *et al.* (1983) suggested that it evolved in the area of the SW Pacific Ocean, and more particularly in the region between Australia and New Zealand, where they encountered it in DSDP samples dating back to the Lower Eocene. The two oldest species that they found in the Lower Eocene, *P. rudis* and *P. robustus* (Whatley *et al.* 1986), were shown to exhibit a considerable resemblance to certain Upper Cretaceous taxa from western Australia. These authors (1983: 497, fig. 2) suggested that *Hermanites sagitta* Bate, 1972, from the Campanian of the Carnarvon Basin, or some similar species, could be the ancestor of *Poseidonamicus*. They argued that *H. sagitta* could have given rise to the hypothetical ancestral *Poseidonamicus* species, which would probably have been sighted, but which gave rise, once the genus had been involuntarily inducted into the deep sea, to all the blind species in the deep-water environments of the world's oceans. Since the two Australian Lower Eocene species are blind (a characteristic of all podocopid ostracods living in waters deeper than about 500 m) then this induction must have taken place at some stage prior to the Eocene.

The same authors suggested, however (1983: 479, fig. 2; 1986: 391), that *P. ocularis* evolved from a fully sighted, shallow, shelf-dwelling ancestor in the Quaternary. *Poseidonamicus ocularis* was only recovered from bathyal environments in the southern part of the area between Australia and New Zealand (DSDP sites 207, 277 and 281) and only from Quaternary strata. They argued (1983: 479) that the discovery of *P. ocularis* 'implies that there has persisted in

shallow waters of this area until recent times a population with eyes, derived direct from a postulated sighted ancestor'. They also comment on the 'exciting prospect that a living sighted species of the genus may be encountered in due course'.

The discovery of the sighted shelf species *P. panopsus* sp. nov. has justified these expectations, but the present authors admit to surprise that it should have been encountered off the southern African Atlantic coast rather than in Australasian waters. Given the Quaternary age of *P. ocularis*, however, it remains quite conceivable that a shallow-water shelf species of the genus remains to be discovered living in the antipodes.

In logic, *P. panopsus* must be considered a lineal descendant of a late Cretaceous or early Palaeogene hypothetical sighted ancestral *Poseidonamicus* species that subsequently give rise to all the blind deep-water and sighted shallow-water species of the genus. Direct contiguity of continental shelf environments between what is now southern Africa and Australasia probably ceased at about 100 m.y. BP (Albian), when southern Africa finally separated from the Falkland Plateau extension of South America (see Dingle *et al.* 1983). Circuitous shallow-water connections probably continued until Turonian times via the Walvis Ridge/Rio Grande Rise archipelago across the South Atlantic, and the Drake Passage shallows between South America and Antarctica but, since the latter date, the two areas have been separated by barriers of abyssal depths. Consequently, the ancestry of *Poseidonamicus panopsus* is uncertain, given the fact that the genus probably arose in Australasia from shallow-water Upper Cretaceous stock. Dingle (1981) discussed the similarity between southern African and western Australian Campanian shallow-water ostracods, and recorded a relatively high similarity (27%) at the generic level. However, there were no species in common, and no evidence suggests any contact between the ostracod populations since at least the mid-Cretaceous. *Hermanites kennedyi* Dingle (Campanian) from SE Africa is similar to *H. sagitta* Bate, a possible progenitor for the SW Pacific *Poseidonamicus* populations (Whatley *et al.* 1983), but even the possibility of homeomorphy from a similar ancestor is not attractive, because there is no record of *Poseidonamicus* in the Tertiary of southern Africa. A lineal connection with the Australasian stocks seems the most likely solution, but it may be that *P. panopsus* or its ancestors do not have a long history on the continental margin of southern Africa, and migrated into the area relatively recently (?late Tertiary) from other areas (such as eastern Africa). Whatever the case, it is remarkable that sighted species have survived so long apart (to the Recent in southern Africa, and to at least the Pleistocene in Australasia) without either becoming extinct or being subject to major evolutionary change. Although this can only be confirmed if and when sighted shelf species of *Poseidonamicus* are recovered from Tertiary shallow-water deposits in the Southern Hemisphere, it does suggest that, when compared to the considerable degree of evolutionary change experienced by deep-water species (Whatley 1985), the genus has been more stable in shallow environments.

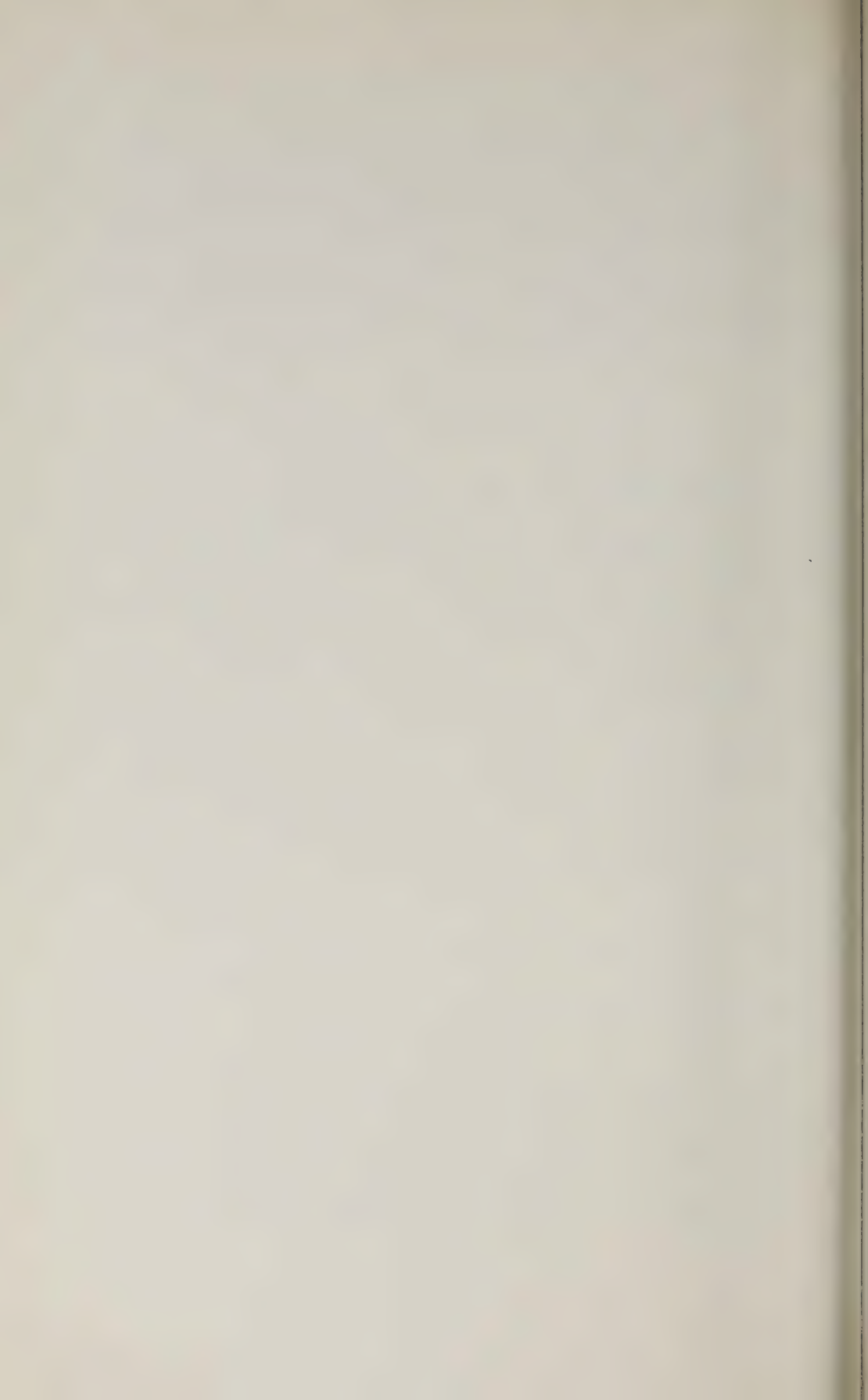
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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family **Nuculanidae**

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers.

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...': '... in *C. namacolus* (Fig. 10) ...'
- The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should preferably be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively. The generic name should not be abbreviated at the beginning of a sentence or paragraph.

Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

R. C. WHATLEY

&

R. V. DINGLE

FIRST RECORD OF AN EXTANT, SIGHTED,
SHALLOW-WATER SPECIES
OF THE GENUS *POSEIDONAMICUS* BENSON
(OSTRACODA) FROM THE CONTINENTAL
MARGIN OF SOUTH-WESTERN AFRICA

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DEEP-SEA SEDIMENTARY ENVIRONMENTS AROUND SOUTHERN AFRICA (SE ATLANTIC & SW INDIAN OCEANS)

by

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M. J. FINCHAM, T. FITTON, B. W. FLEMMING, R. I. GENTLE, S. W. GOODLAD, A. K. MARTIN,
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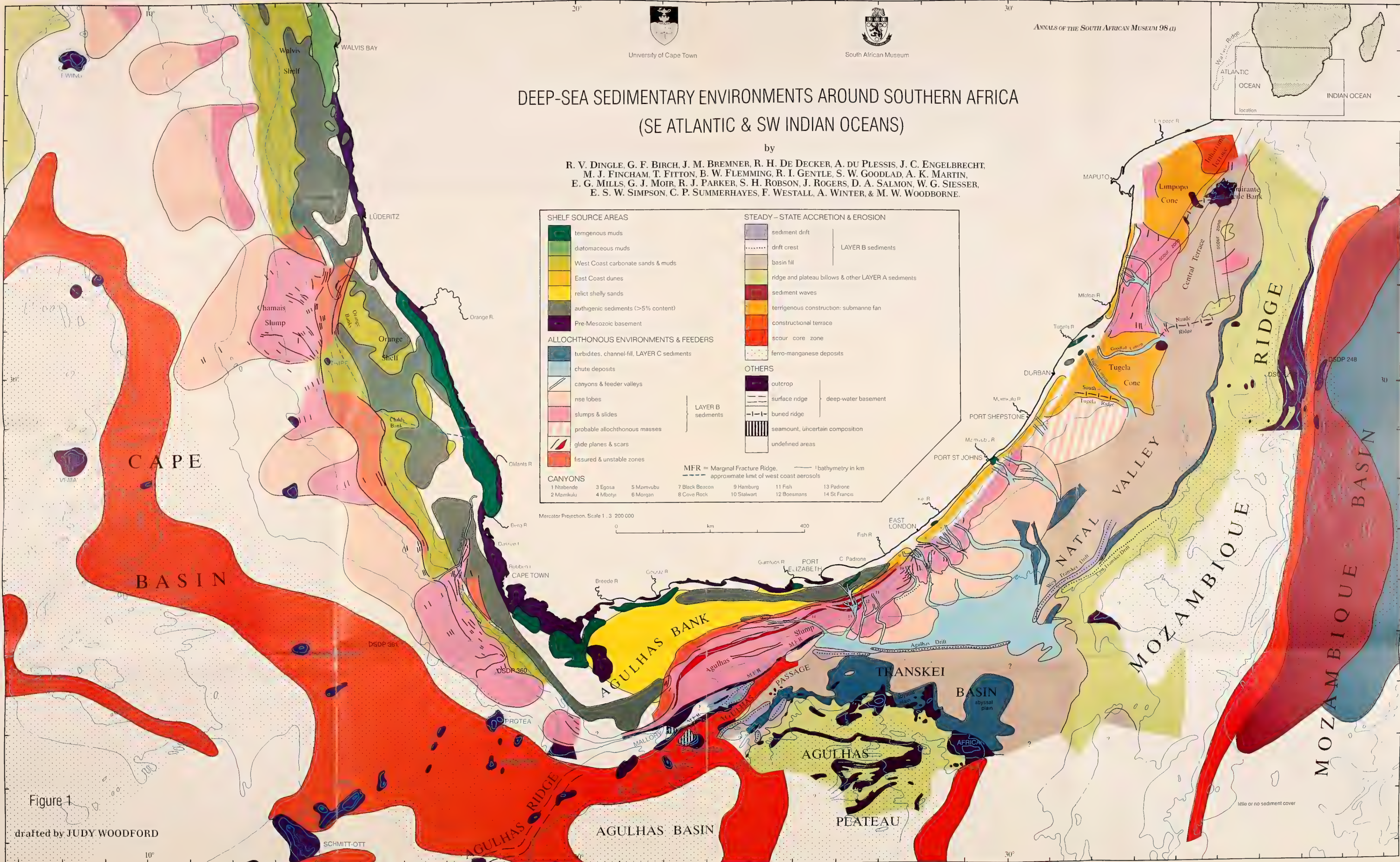
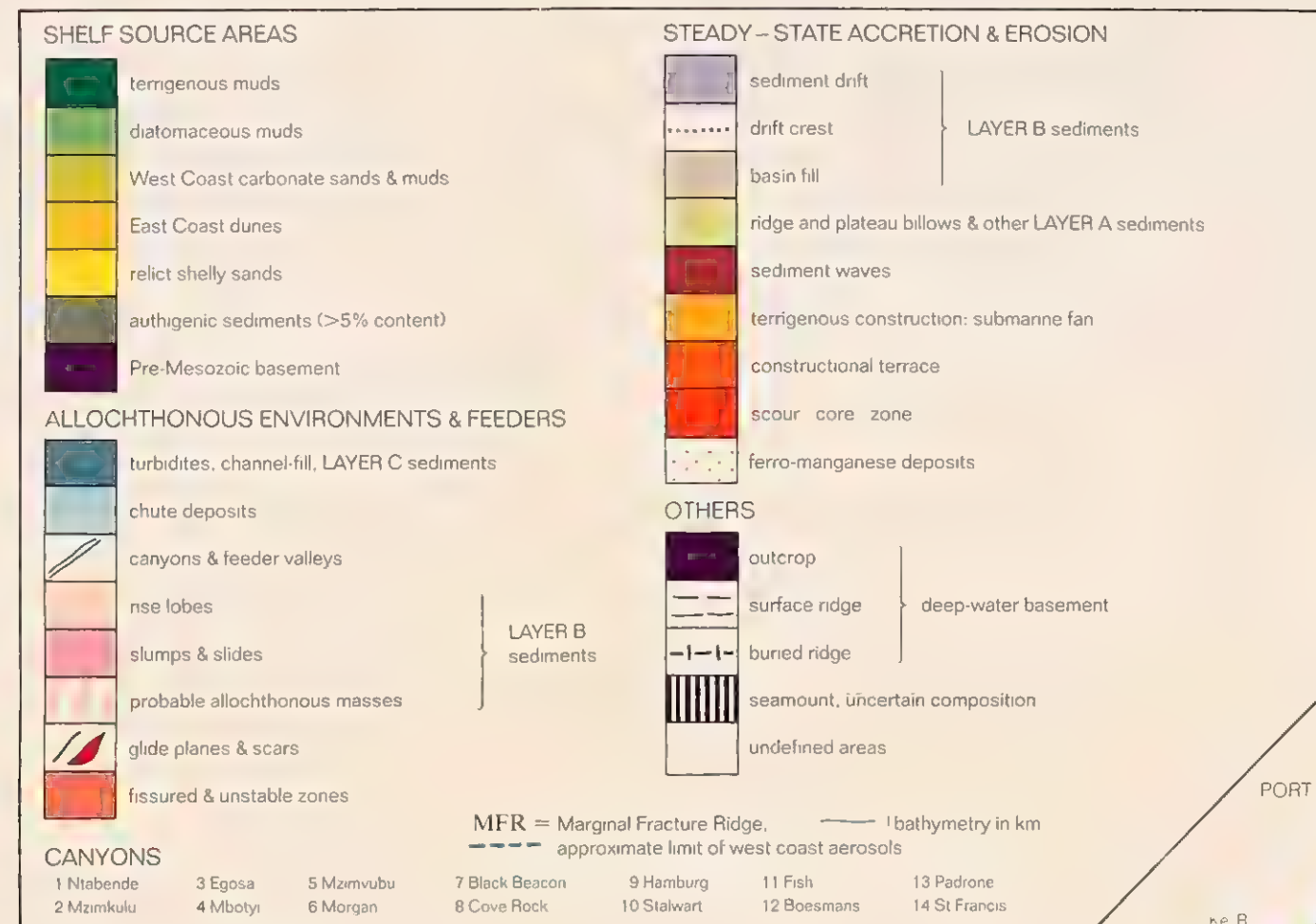


Figure 1

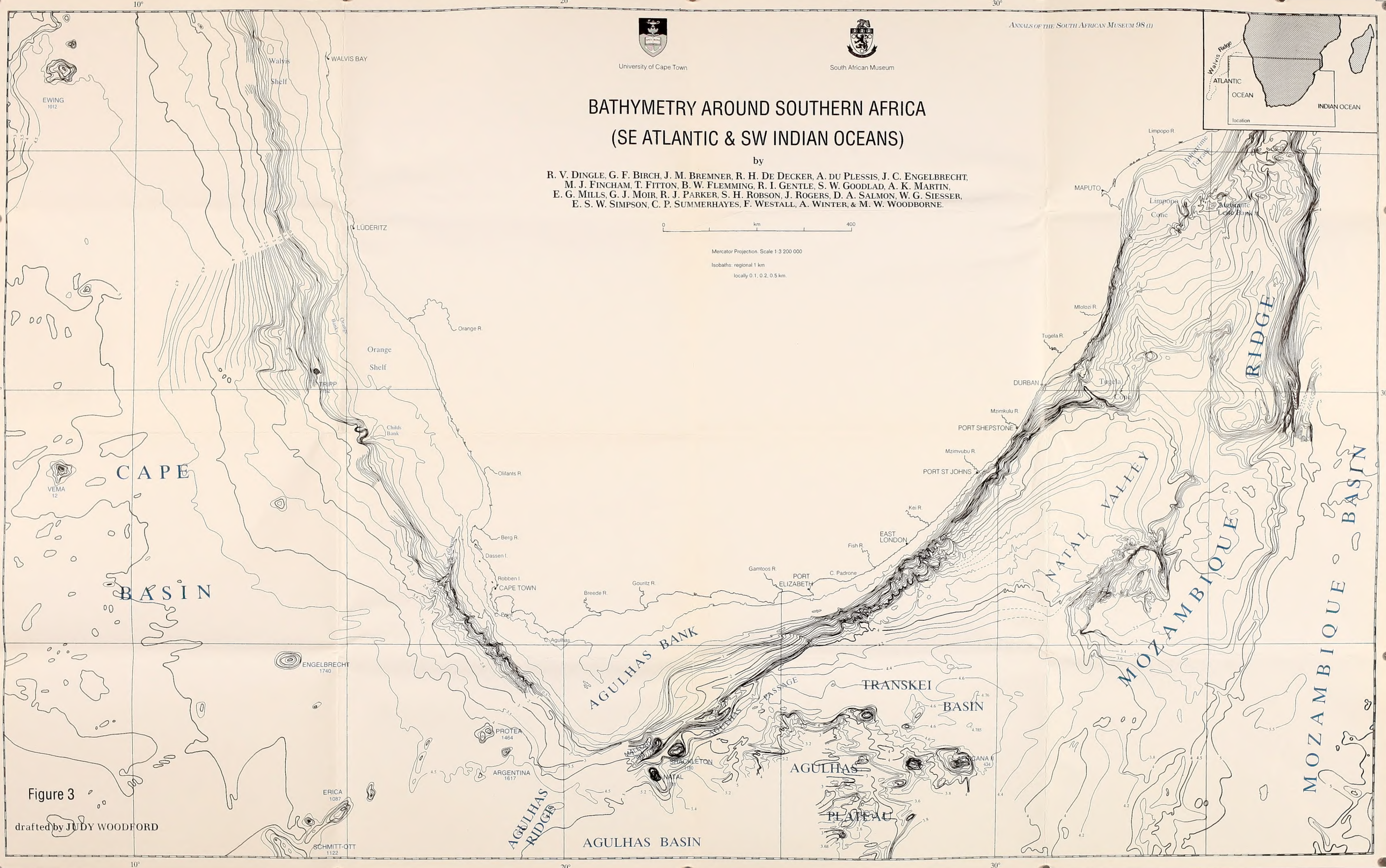
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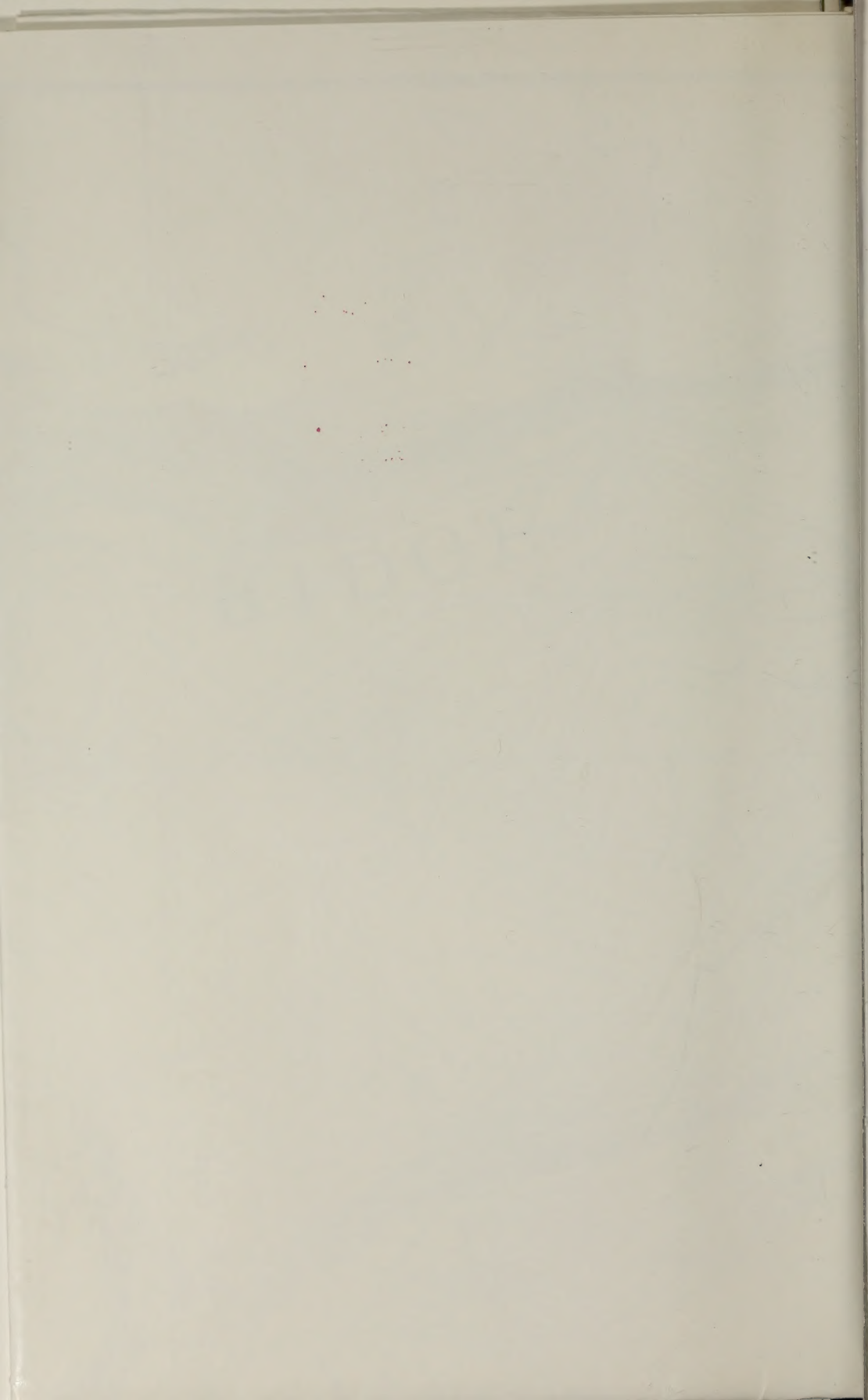
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